

TWO NEW DICYNODONTS FROM THE
TRIASSIC NTAWERE FORMATION, ZAMBIA

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TWO NEW DICYNODONTS FROM THE TRIASSIC NTAWERE FORMATION, ZAMBIA

By CHRISTOPHER BARRY COX

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SYNOPSIS

Two new types of dicynodont from the upper fossiliferous horizon of the Ntawere Formation of Zambia are described. The first, *Zambiasaurus submersus*, is represented by the fragmentary remains of at least eighteen juveniles and one adult, all of which were apparently drowned in a sudden flood. *Zambiasaurus* is a stahleckeriid closely related to, and probably directly ancestral to, *Stahleckeria* of the Middle Triassic of Brazil. It is the earliest known stahleckeriid, and the first known outside South America. The earlier history of the group is unknown.

The other new dicynodont, *Sangusaurus edentatus*, is known only from a few fragments of the skull. It is a kannemeyeriid, and shows some similarities to *Ischigualastia* of the Middle or Upper Triassic of Argentina.

Both the faunas of the Ntawere Formation appear to be intermediate in age between the Cynognathus Zone fauna of South Africa and the Manda fauna of East Africa. Its age, in terms of the standard Triassic sequences, is provisionally estimated as lowermost middle Triassic (Lower Anisian).

I. HISTORICAL INTRODUCTION

THE Luangwa River is a major tributary of the Zambezi River, and is the main river of the eastern half of Zambia. Fossil reptiles were first found in the upper Luangwa River valley by Prentice in 1925, and the area was reconnoitred and later investigated by Dixey in 1928 and 1935 (see Dixey 1936, 1937). He recorded fossil reptiles from six different horizons within the Karroo succession, and also from a higher horizon which he named the "Dinosaur Beds" and which he regarded as Cretaceous in age.

The upper Luangwa River valley is remote, and is inaccessible to vehicles unless these can negotiate rough dirt tracks. As a result, the area was not re-examined until 1960 and 1961, when Dr. A. R. Drysdall of the Geological Survey of Northern Rhodesia, and James Kitching, Field Officer of the Bernard Price Institute for Palaeontological Research of Witwatersrand University, spent a total of four months in the area. They examined the area north-west of the small village of Sitwe, on the River Luwumbu, 125 miles north of Lundazi, the administrative centre of this north-eastern portion of the Eastern Province of Zambia. They confirmed that the area was rich in fossil reptiles, and collected nearly 500 specimens.

Karoo fossils were, of course, originally found in South Africa, and many of the early specimens were sent to the British Museum (Natural History) in London for appraisal and description. The resulting collection is of historic interest and contains many type specimens, but many are imperfect and most of them are poorly documented and lack post-cranial elements. It was therefore decided to mount a major expedition to Africa, with the aim of making a large and representative collection of fossil Permian and Triassic vertebrates, using up-to-date methods of collecting and recording full details as to their localities and stratigraphical origin. In view of the known richness of the area, it was decided to rely upon the upper Luangwa River valley for the collection of the bulk of the Permian fossils, and afterwards to visit the south-western region of Tanganyika, where fossil vertebrates of both Permian and Triassic age were known to occur.

The resulting expedition, the British Museum (Natural History) and University of London Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika, spent six weeks collecting in the Sitwe area in the summer of 1963, and a preliminary account of the results has been published (Attridge, Ball, Charig & Cox 1964). The expedition was greatly helped by the presence of James Kitching, whose services had been very kindly loaned by the Bernard Price Institute. As a result there was no difficulty in finding the fossil localities, once the necessary tracks for vehicle access had been constructed, and a total of 220 specimens, weighing some $2\frac{1}{2}$ tons, was collected.

II. STRATIGRAPHY

As a result of their examination in 1960–61, Drysdall & Kitching were able to give a detailed account of the stratigraphy and geology of the area (Drysdall & Kitching 1963), from which the details in this section are taken.

Some alterations to Dixey's earlier interpretation of the stratigraphy of the area became necessary. Drysdall & Kitching found that all of Dixey's six Karroo horizons were part of a single richly fossiliferous formation, which they named the Madumabisa Mudstone. The fauna of this is identical with that of the Lower Beaufort *Endothiodon* and *Kistecephalus* zones of South Africa.

Above the Madumabisa Mudstone, and separated from it by an hiatus of probably minor nature, Drysdall & Kitching defined a major lithological unit which they have subdivided to give three formations of more convenient thickness. The lowest, the Escarpment Grit, is of varying thickness (230– over 700 feet), whilst the uppermost, the Red Marl, is 230–400 feet thick. Between the two lies the Ntawere Formation, again of varying thickness (400– over 3,500 feet) and consisting of a succession of thin, alternating arenaceous and argillaceous beds. The whole unit is subdivided into formations on the basis of the different proportions of mudstone and grit.

Above the Red Marl lies the non-fossiliferous Upper Grit, over 3,000 feet thick; in some places the two are separated by a thin transition zone of intercalated grits and mudstones, while in others there is a sharp transition.

Drysdall & Kitching found two fossiliferous horizons in the Ntawere Formation and Red Marl. The lower horizon lies within the Ntawere Formation; its fauna

consisted predominantly of large dicynodonts, with fairly common large amphibians, and also yielded an excellent *Diademodon* skull which has already been described (Brink, 1963). The upper horizon comprised the uppermost beds of the Ntawere Formation and the lower part of the Red Marl; its fauna contained the remains of both vertebrates and molluscs.

Drysdall & Kitching consider that Dixey's "Dinosaur Beds" can only be identified, both lithologically and geographically, with the fossiliferous Ntawere Formation. Dixey based his assessment of the "Dinosaur Beds" upon some large, fragmentary, rolled bones which he found *in situ* and which Swinton tentatively identified as possibly dinosaurian. However, Drysdall & Kitching found no bones *in situ* at the localities indicated on Dixey's map, but they were able to identify a thin superficial pebble deposit which Dixey regarded as the last débris of the almost completely eroded Dinosaur Beds. This pebble deposit contained large fragmentary bones, mostly identifiable as dicynodont. Bones of comparable size and appearance are common in the nearby Madumabisa Mudstone, so that the bones found in the pebble deposit are probably derived fossils originating in the Madumabisa Mudstone. The bones observed *in situ* by Dixey have not been relocated and may also have been derived fossils. Alternatively they may have come from as yet unrecognized fossiliferous beds of the Ntawere Formation, which is now known to contain pseudo-suchians—whose remains are not readily distinguishable from those of dinosaurs.

The fossiliferous beds themselves are dark red, soft mudstones, with feldspathic grit bands. Bones almost always occur individually; no articulated remains have been found. The bones are usually cracked and weathered, suggesting prolonged exposure before burial; they are often covered with a purple-red layer of haematite, or with a thick layer of calcite. Fragments of bone are common in some of the grit bands, and may be the remains of skeletons disarticulated by shortlived floods which were responsible for the coarser sediment forming the grit bands.

Drysdall & Kitching state (1963 : 22) that amphibians and molluscs (*Unio karooensis*) are present towards the base of the upper fossiliferous horizon, where the commonest reptiles are the cynodonts. The cynodonts persist into the higher levels, where the predominant reptile is now a large dicynodont, where the reptiles outnumber the amphibians, and where the molluscs are now rarer. One of the cynodonts has already been described (Brink, 1963) as *Luangwa drysdalli*.

The fossils are found in the systems of small gulleys and eroding flats at the upper ends of the small tributaries of the River Sangu. Each of the dicynodont genera described in this paper was found in an individual collecting area of this kind, within the general area described as "locality 15" by Drysdall & Kitching, and hence within the upper fossiliferous horizon. During the 1963 expedition we were not able to define the stratigraphic inter-relationships of these individual areas, so that the positions, within this horizon, of the two dicynodont genera described here are not known.

Fossils from the Ntawere Formation are usually fairly scarce and covered with layers of haematite or calcite. The *Zambiasaurus* material makes an outstanding exception to this rule: a portion, about ten yards long and seven yards wide, of the

side of a small ridge was found to be strewn with fragments of bone, nearly all of which were completely free from matrix. The whole area was stripped of vegetation and swept clean, with the result that 500–600 fragments of bone were collected. Though no bones could be found *in situ*, some of the fragments were embedded in pieces of coarse, unsorted, highly feldspathic grit. The proportion of the alkali feldspar, quartz and mafic minerals suggests that the parent rock was of granite composition. The poor sorting and lack of rounding of the grains, and unaltered condition of the feldspar, suggests rapid deposition. The whole collection was therefore deposited by one of the floods mentioned above.

III. SYSTEMATIC DESCRIPTIONS

Genus *ZAMBIASAURUS* nov.

The new genus has been named *Zambiasaurus* after the new name of its country of origin.

GENERIC DIAGNOSIS: Large dicynodont: the composite restored immature skull is 23 cm. long and 21 cm. broad, while the adult might have had a skull about 45 cm. long and 40 cm. broad. No teeth in upper or lower jaws. Greatest width of skull is across occiput; skull tapers anteriorly. Wide inter-orbital region, narrow intertemporal region. Blunt snout. Short median suture between nasals. Preparietal bone absent; pineal foramen completely surrounded by parietals. Parietals are slightly concave antero-posteriorly and form bulk of intertemporal bar. No sharp median intertemporal ridge. Interparietal bone does not extend far forwards. Sharp transition between dorsal and occipital surfaces. Occipital wings of squamosal extend laterally and somewhat posteriorly. Palatal surface of premaxilla bears pair of anterior ridges.

At least four sacral ribs. Scapular blade tall and narrow, with low ridge running up antero-external edge; acromion process probably poorly developed. Coracoid foramen wholly within precoracoid bone. Small pubis.

TYPE SPECIES: *Zambiasaurus submersus* sp. nov.

MATERIAL: Unless otherwise stated, all specimen numbers refer to the collection deposited in the British Museum (Natural History).

The bone fragments were mainly parts of the post-cranial skeleton. Apart from unidentified fragments and portions of ribs, the collection included:

Vertebral centra	.	.	.	58	Ulna	29
Sacral ribs	.	.	.	7	Ilium	40
Scapula	.	.	.	39	Ischium	16
Coracoid	.	.	.	13	Pubis	9
Precoracoid	.	.	.	4	Femur	51
Clavicle	.	.	.	6	Tibia	24
Sternum	.	.	.	3	Fibula	13
Interclavicle	.	.	.	—	Metapodials, podials etc.	15
Humerus	.	.	.	68	Premaxillae	4
Radius	.	.	.	19	Maxillae	9

Nasals	2	Quadrates	2
Frontals	6	Squamosals	27
Postorbital	1	Dentaries	2
Intertemporal region	8	Articular region of lower jaw	10
Braincase elements	8	Other fragments of lower jaw	6

As found, none of the limb bones was complete, but it was subsequently found that the fragments included the whole of an ulna, two femora and two tibiae. Apart from a few cynodont bones, and one other exception discussed below, there is no variation in the morphology of the bones, which therefore appear all to belong to a single species of dicynodont. This species is represented by the remains of at least eighteen individuals, as there are eighteen right distal ends of humeri; however, it is almost certain that there was really a somewhat greater number of individuals, all of which are only incompletely represented. These individuals come from a fairly restricted size range; in the humeri, for example, the proximal ends are from 8.5 to 10.0 cm. across and the distal ends are from 7.8 to 11.0 cm. across.

In addition to these individuals, there are the remains of a single individual of considerably larger size, the distal end of whose humerus is 17 cm. across. This specimen could be regarded either as a larger member of the same species as the numerous smaller individuals, or as belonging to a different, larger species.

There are several reasons for believing that the many smaller individuals are immature forms, and that the single large individual represents the adult of the same species. The immaturity of the small specimens is indicated by the lack of co-ossification and sutural union of the skull bones (even the bones of the braincase have not become firmly united) and by the poorly defined nature of the articular surfaces of the limb bones. On the humerus, for example, the articular areas for the glenoid, radius and ulna are hardly defined at all, while the articular surfaces of the radius, tibia and fibula are almost featureless and give the impression of having been covered in life with a thick capping of cartilage. Such surfaces on this and other bones have a characteristic appearance: the surface is smooth but interrupted by a large number of tiny round holes, the edges of which are often slightly raised, giving the appearance of tiny volcanic craters. In living reptiles this appearance is characteristic of surfaces covered by cartilage, and it will be referred to as "cartilage ornament" in the descriptive sections below.

The bones of the larger individual, on the other hand, have very well developed articular areas, but are otherwise identical with those of the smaller individuals. It is therefore regarded as the adult of the species, but is described separately, after the smaller individuals have been described, so as to facilitate any taxonomic change in its status, should this subsequently be found necessary.

A death-assemblage composed of a single adult and many juveniles is rather unusual. The flood which deposited the accompanying coarse grit may provide a possible explanation; it is conceivable that such a flood might cause a heavy mortality in the young dicynodonts, but that only a few of the larger adults would be caught and overwhelmed. The adult might even be a carcass of an individual which had died recently and which was caught up by the flood waters.

Zambiasaurus submersus sp. nov.

Text-figs. 1-20

The specific name *submersus* refers to the likelihood that the specimens were drowned.

HOLOTYPE OF *Z. submersus*: Livingstone Museum (Zambia) specimen No. LM/NH 9/2, consisting of interparietal, left parietal and part of left squamosal of presumed immature individual.

PARATYPES: British Museum (Natural History) catalogue Nos. R.9001-R.9140; Livingstone Museum (Zambia) specimen Nos. LM/NH 9/3-9/35.

HORIZON AND LOCALITY: Upper fossiliferous horizon of Triassic Ntawere Formation: from locality 15 of Drysdall & Kitching (1963), about 3½ miles west of Sitwe, in the upper Luangwa Valley, Eastern Province, Republic of Zambia (Field No. 15 A/1).

DESCRIPTION. As explained below the original skull morphology has had to be reconstructed and deduced from the eighty-five fragments listed above.

The most extensive fragment, which has been designated as the type specimen (Livingstone Museum specimen no. LM/NH 9/2; cast in B.M.(N.H.) is R.9000) comprises an interparietal, left parietal and part of the left squamosal (Text-fig. 1, b-e). The right parietal has become detached and lost, so that the sutural surfaces by which it was attached to the interparietal and left parietal are visible. It can therefore be seen (Text-fig. 1d) that the interparietal does not extend far forwards between the two parietals. The interparietal also does not extend far laterally before it joins the squamosal, neither does it overlap the occipital surface of the squamosal to any great extent. Though there is a sharp transition between the dorsal surface of the intertemporal bar and the posterior surface of the interparietal, there is also a recessed area in the dorso-median region of the interparietal, where the nuchal ligaments were presumably attached. Below this recess lies the occipital surface of the interparietal, in which there is a pair of nutrient foramina.

The dorsal surface of the left parietal is smooth and slightly concave antero-posteriorly. Though it is also slightly concave transversely, so that there would have been a very slight median ridge, the intertemporal bar as a whole is flattened, rather than forming an inverted V shape. The dorsal and lateral surfaces of the parietal meet at an acute angle (about 60°) and the lateral surface is shallowly concave dorso-ventrally. The posterior end of the lateral surface of the parietal is slightly damaged, but extended back to overlap the squamosal. The upper part of the lateral surface of the parietal is slightly recessed and bears the pitted and grooved ornament characteristic of a surface overlapped by another bone. There can be no doubt that this surface was covered by the posterior extension of the post-orbital. Another specimen (R.9020) shows this surface even more plainly, and it is clear that the postorbital extended back as far as the junction between the parietal and the interparietal.

The parietal in the holotype forms the whole of the border of the left half of the pineal foramen (Text-fig. 1b). Another specimen (R.9020) in which this region is slightly better preserved, shows that the parietal forms a thin strip of the dorsal surface both lateral to, and anterior to, the pineal foramen (Text-fig. 1a). In neither specimen is there any trace of a suture delimiting a separate preparietal bone, and this bone must have been absent.

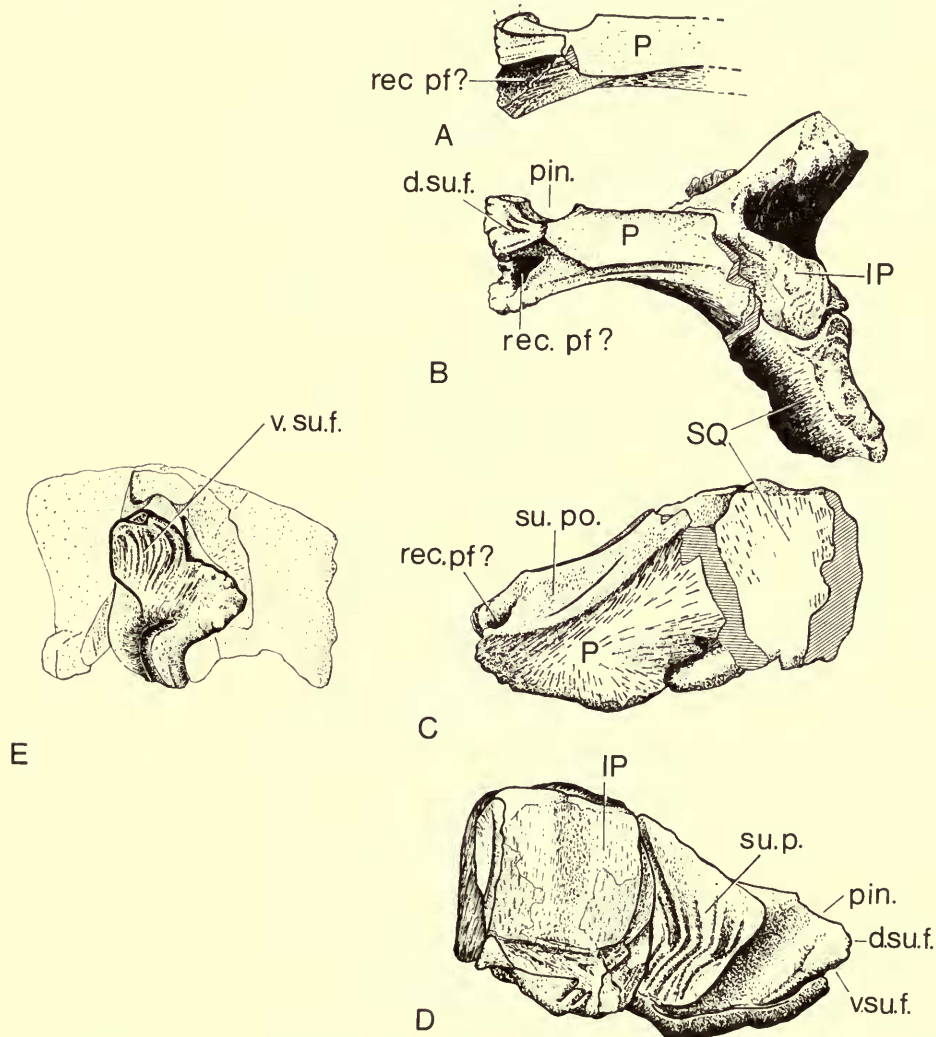


FIG. 1. *Zambiasaurus submersus* gen. et sp. nov., juvenile. $\times \frac{2}{3}$. A, dorsal view of anterior end of left parietal, R.9020. B-E, holotype (Livingstone Museum No. LM/NH 9/2) in B, dorsal view; C, lateral view; D, medial view; E, anterior view. Abbreviations: d.su.f., dorsal sutural area for frontal; IP, interparietal; P, parietal; pin., pineal opening; rec.pf?, recess for ?postfrontal; SQ, squamosal; su.p., sutural area for right parietal; su.po., sutural area for postorbital; v.su.f., ventral sutural area for frontal.

Much of the anterior end of the dorsal surface of the parietal is covered by ridged, grooved and pitted areas of overlap (Text-fig. 1a, b). The most medial of these areas must have received the posterior end of the frontal (Text-fig. 1a, b) which therefore reached as far posteriorly as the level of the posterior border of the pineal foramen and also approached very close to its lateral and anterior borders (Text-figs. 1a, 2b, 2ob). The most lateral area of sutural overlap on the antero-dorsal region of the parietal is that for the postorbital. Between this and the area for the frontal there is a deep posteriorly-directed recess (Text-fig. 1a-c: rec.pf?). This

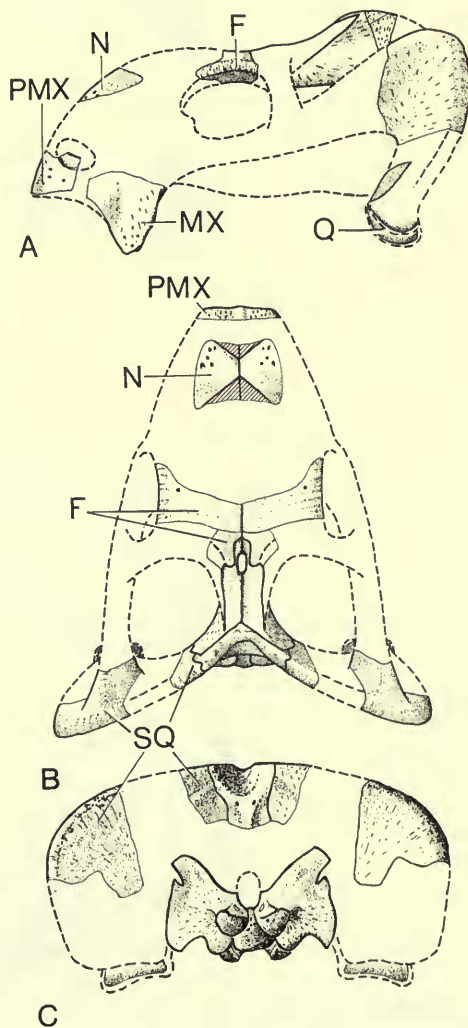


FIG. 2. *Zambiasaurus submersus* gen. et sp. nov. Drawings showing relationships of preserved fragments of skull to reconstruction of complete juvenile skull. $\times \frac{1}{4}$. A, lateral view; B, dorsal view; C, occipital view. Abbreviations: F, frontal; N, nasal; MX, maxilla; PMX, premaxilla; Q, quadrate; SQ, squamosal.

recess may have received a small separate postfrontal bone. If it was present, this bone may have been concealed by a superficial meeting between the postorbital and the frontal.

There is a considerable angle between the more posterior part of the parietal and those areas to which the frontal attached. This fact, and the concave outline of the dorsal edge of the parietal in lateral view (Text-fig. 1c), suggests that the intertemporal bar projected postero-dorsally above the level of the rest of the dorsal surface of the skull (Text-fig. 2a). This is confirmed by fragment R.9014 (Text-fig. 3a), which comprises the region around the front end of the pineal foramen. The line of the dorsal edge of the intertemporal bar apparently continued forwards for a short distance on to that part of the frontal which lies antero-lateral to the pineal foramen, for this part of the bone is slightly thickened above the level of the rest of the frontal. This fragment also confirms that there is no preparietal bone and that the frontal overlaps the anterior end of the parietal. The frontal also extends posteriorly for a short distance under the parietal, where there is a wide sutural union between these two bones (Text-fig. 1d, e: v.s.u.f.).

The morphology of the area immediately in front of the pineal foramen, including the interorbital width, is shown by specimen R.9015. This is a large piece of a right frontal, including both the midline suture and part of the edge of the orbit. Specimen R.9016 is an almost identical fragment of a left frontal, on the postero-medial region of which can be seen the suture for attachment to the parietal. This fact is important, for it establishes the relationship between these frontal fragments, including the upper margin of the orbit, and the intertemporal bar. The resulting position of the orbit is relatively far back, so that the posterior edge of the post-orbital bar is at the level of the pineal foramen.

It is possible, but not certain, that the most antero-lateral corner of the frontal fragment R.9015 bears a short stretch of the surface to which the prefrontal bone was attached. Even if it does not, the suture cannot have been far anterior to this point, since that bone normally forms the antero-dorsal corner of the orbit.

Specimen R.9012 is part of a right nasal bone (Text-fig. 3b, c). The bone was overlapped postero-medially by the anterior end of the frontal, and antero-medially by the posterior end of the premaxilla. These surfaces are separated by only a short median sutural surface for the left nasal. In another, slightly larger, right nasal fragment (specimen R.9013) the overlap surfaces for the premaxilla and frontal meet, completely covering the median suture between the two nasals. The antero-lateral corner of these nasals bears a number of foramina.

The dorsal surface of the nasal R.9012 consists of two planes, which meet along a line which runs antero-laterally. The more postero-lateral plane faces dorso-laterally and represents the lateral surface of the snout. The anterior plane faces antero-dorsally and represents the beginning of the down-turning of the snout. This plane provides a clue as to the relative position of the nasal and of the anterior end of the snout since, together with the anterior surface of the premaxilla, it must form a smooth curve when seen in lateral view (Text-fig. 2a). Some hint as to the distance between the nasal and the anterior end of the premaxilla is also provided by the angle of the suture between these two bones, as seen along the front surface of

the nasal. In most dicynodonts this suture runs to the antero-dorsal corner of the nostril in an almost straight line.

The front edge of the premaxilla is blunt, running transverse to the main axis of the skull. The grooves which lie lateral to the paired anterior palatal ridges therefore run on to the anterior edge of the premaxilla (specimen R.9001; Text-fig. 3d).

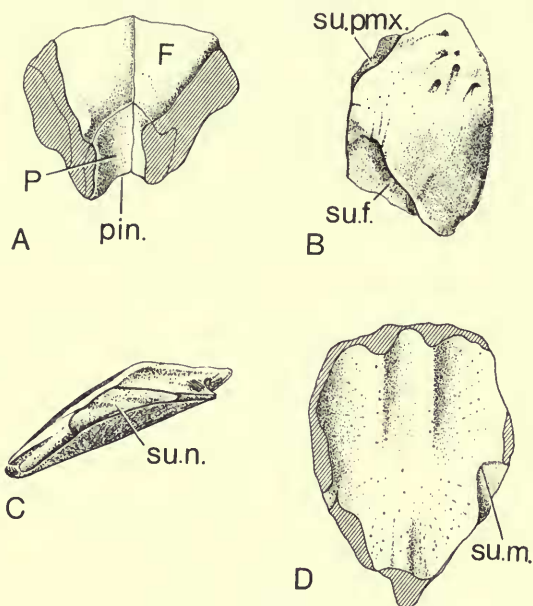


FIG. 3. *Zambiasaurus submersus* gen. et sp. nov., juvenile. $\times \frac{2}{3}$. Dorsal view of fragment R.9014 comprising area around anterior end of pineal foramen. B, C, fragment of right nasal (R.9012) in dorsal (B) and medial (C) views; D, ventral view of premaxilla (R.9001). Abbreviations: F, frontal; P, parietal; pin., pineal foramen; su.f., sutural area for frontal; su.m., sutural area for maxilla; su.n., sutural area for left nasal; su.pmx., sutural area for premaxilla.

There is little difficulty in fitting a maxilla (e.g. specimen R.9004) to the premaxilla. All nine maxillae are tuskless. Like the premaxilla and the anterior part of the nasal, the maxilla bears a number of nutrient foramina. There is a slight posteriorly directed flange down its postero-lateral edge.

At no point is there any junction between the preserved parts of the nasal-premaxilla-maxilla section and the more posterior section of the skull. It was therefore only possible to attempt to estimate the original relationship between these two sections by assembling each independently in a plasticine matrix and then matching them together, keeping the palatal surface of the premaxilla horizontal. The reconstruction shown appears quite plausible and does not violate any known normal feature of dicynodont morphology. Nevertheless, the exact distance between

the two sections (and therefore the exact length of the frontal) must remain in doubt.

At the other end of the skull, there is similarly no certain relationship between the intertemporal-interparietal region and the remainder of the squamosal and braincase (Text-fig. 2). Most of the fragments of squamosal comprise the region where the zygomatic arch arises from the front surface of the occipital wing. The orientation of the base of the zygomatic arch, and also the orientation of the piece of squamosal attached to the interparietal of the type specimen (Text-fig. 1b) show that the squamosals extended laterally and somewhat posteriorly from the midline. The approximate width across the occiput follows from the interorbital width, since the zygomatic arches must have continued anteriorly and somewhat medially into the suborbital bar.

The fragments of braincase include a good basioccipital-basisphenoid (specimen R.9027) and a good exoccipital-opisthotic-prootic (specimen R.9028). The occipital condyle is of the normal tripartite dicynodont pattern. The tuber around the fenestra ovalis is formed partly by the basisphenoid and partly by the opisthotic. The opisthotic also forms the whole of the distal end of the paroccipital process; its anterior surface is covered by the prootic. Dorso-laterally, both the prootic and the opisthotic end abruptly in a thick surface, the ornament of which shows that it was capped by cartilage, and which presumably met the squamosal. The dorsal edge of the opisthotic, which slopes upwards and outwards, bears a similar ornament and must have joined the supraoccipital. The medial surface of the prootic and opisthotic bears the excavation for the inner ear.

The quadrate is of usual dicynodont type. Once again, its exact relationship to the remainder of the skull is uncertain, and it has merely been placed in the position normal in the group, at about the same level as the ventral margin of the premaxilla and ventro-lateral to the distal end of the paroccipital process.

Most of the fragments of lower jaw are of the articular region, which is of normal dicynodont type. Two fragments of the front end of the dentary (specimens R.9039, 9040) show that this was wide and blunt, as might have been expected from the shape of the premaxilla.

Postcranial morphology. To facilitate comparison, all bones are illustrated as viewed from the left side. Where necessary, bones from the right side have been reversed in the drawings so as to appear as left side bones.

There is a considerable number of fragmentary *vertebrae*. The prezygapophyses are usually concave, the postzygapophyses convex. The antero-dorsal corner of the lateral surface of the centrum bears a small facet for the lower end of the rib head. The remainder of the facet for the rib head extends postero-dorsally up the side of the neural arch. This facet extends to a varying degree up the ventral surface of the transverse process, which is dorso-laterally directed.

It is not possible to obtain any useful information from the fragments of *ribs*.

The *scapula* illustrated (Text-fig. 4) is reconstructed from two complementary fragments: a lower fragment (R.9068) and an upper fragment (R.9069). The blade is very long and narrow. There is a rather low scapular spine which runs for some distance up the antero-lateral edge of the bone (Text-fig. 4b) but which does not

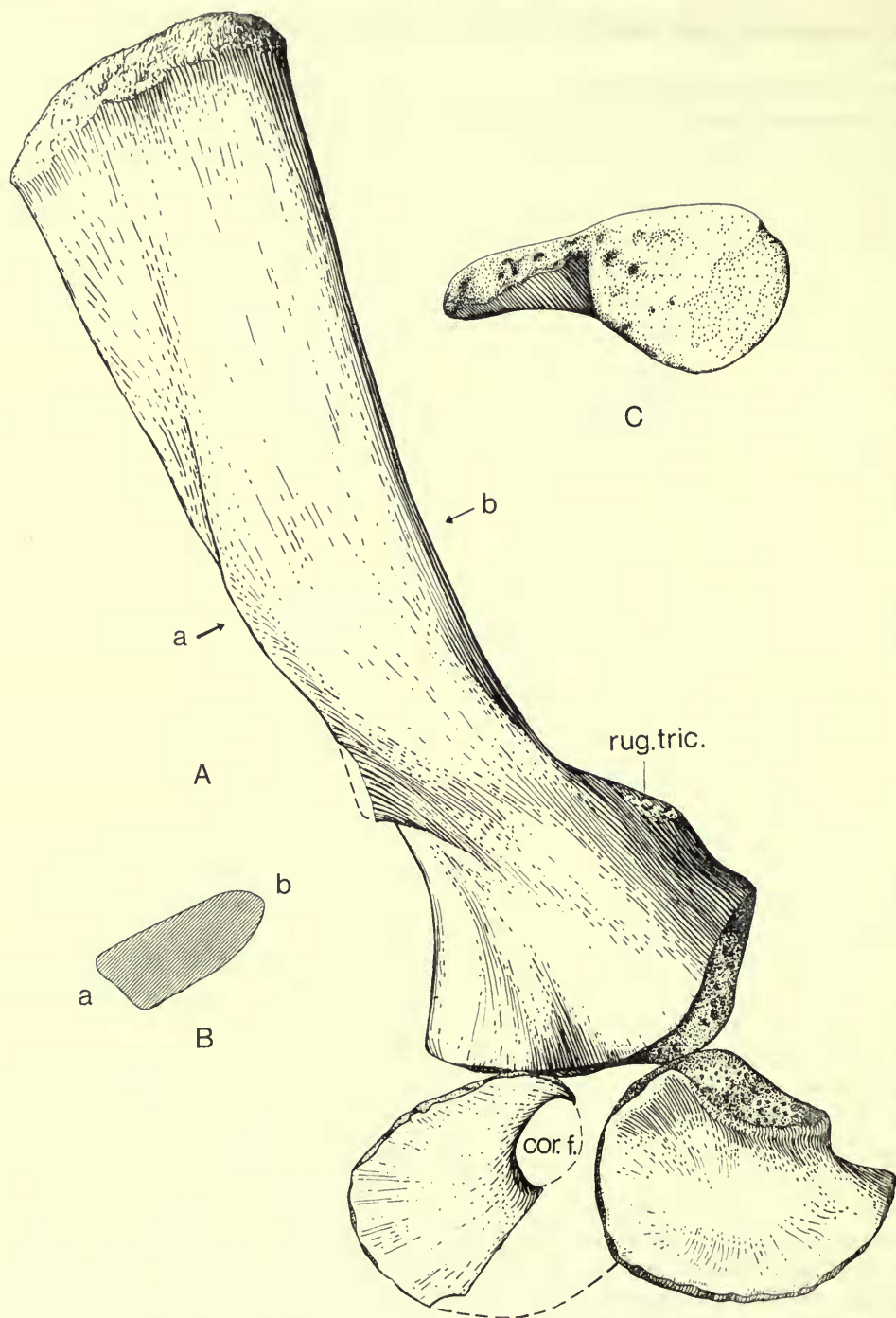


FIG. 4. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Composite restoration. A, lateral view of scapula, precoracoid and coracoid (scapula and precoracoid are composite reconstructions); B, section through scapula at level a-b; C, view of ventral end of scapula, lateral surface uppermost. $\times \frac{2}{3}$. Abbreviations: cor.f., coracoid foramen; rug. tric., rugosity for ligament of triceps muscle.

reach its upper end. The acromion process is damaged, but does not appear to have been very large. There is a pronounced rugose area on the postero-dorsal edge of the scapula a short distance above the glenoid; this is probably the area of

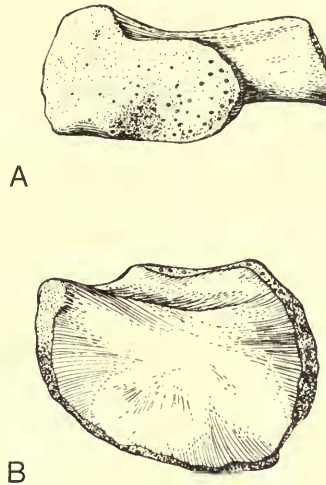


FIG. 5. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Coracoid in A, dorsal view and B, medial view. $\times \frac{2}{3}$

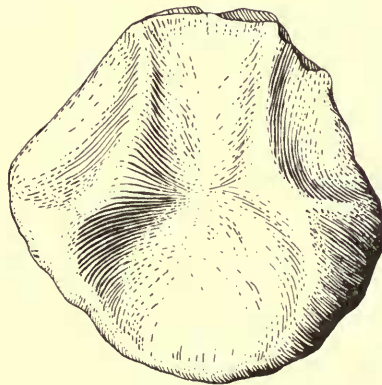


FIG. 6. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Sternum in dorsal view. $\times \frac{2}{3}$.

origin of the scapular ligament of the triceps muscle. The glenoid surface is sub-circular, but the surface for attachment of the precoracoid is quite thin (Text-fig. 4c).

The *coracoid* illustrated (specimen R.9073; Text-figs. 4, 5) is probably from a somewhat smaller individual than the scapula illustrated, as the scapular facet on the coracoid is narrower than the coracoid facet on the scapula. The outlines of these two surfaces do not, in any case, match; this is probably because there was

still much cartilage between the elements of the girdles of these presumably juvenile individuals.

The *precoracoid* (Text-fig. 4) is incomplete; it is restored from three incomplete specimens (R.9078-80). Part of the edge of the coracoid foramen is preserved; since there is no notch in the lower edge of the scapula, this foramen must have lain wholly within the precoracoid.

Though a few fragments of *clavicle* are preserved, these give no useful information about the bone. No fragments of *interclavicle* have been identified.

The *sternum* (Text-fig. 6) is roughly hexagonal in outline. Its ventral surface is slightly concave. On its dorsal surface lie a pair of postero-lateral bosses, on the ends of which can be seen cartilage-ornament. These bosses probably gave insertion to the ventral ends of the anterior thoracic ribs.

Since no complete *humerus* is known, it has reconstructed mainly from two complementary fragments, a proximal fragment R.9088 and a distal fragment R.9089

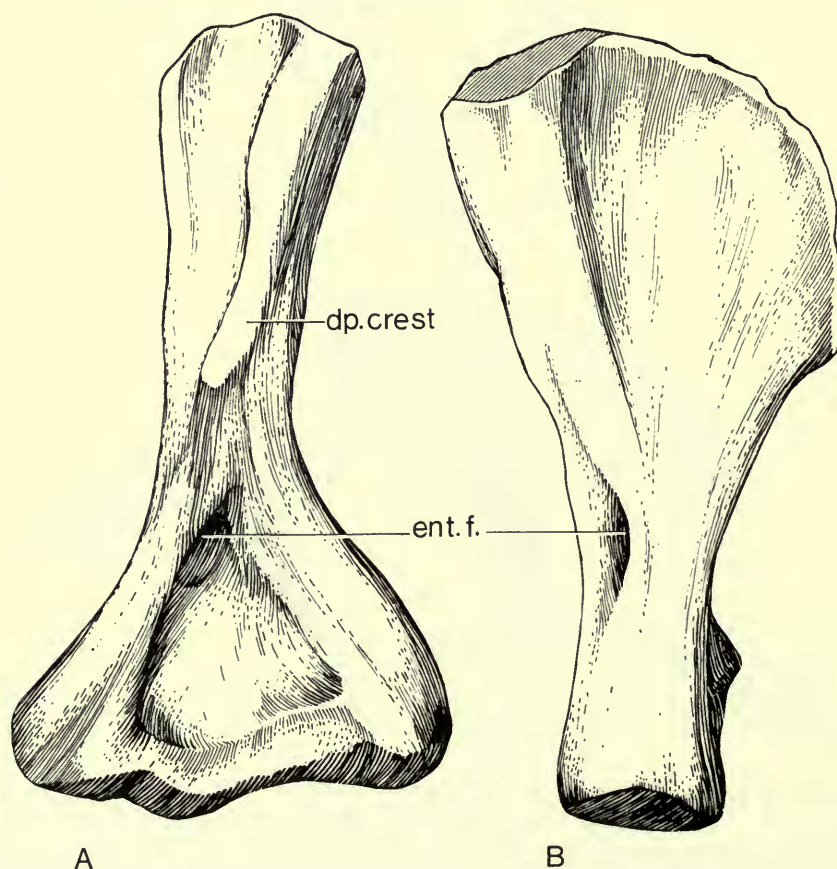


FIG. 7. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Composite restoration of humerus in A, ventral view and B, posterior view. $\times \frac{2}{3}$. Abbreviations: dp.crest, deltopectoral crest; ent.f., entepicondylar foramen.

(Text-figs. 7, 8). It is strongly twisted. As in all the limb-bones, the areas of muscular insertion and of articulation are poorly defined, as might be expected in juvenile animals. There is thus little trace of the proximal condyle, nor of the condyles for the radius and ulna. Traces of cartilage-ornament can be seen over many of these surfaces, proving that the absence of the condyles is not due simply to erosion.

No complete *radius* is known, and the bone has been reconstructed (Text-fig. 9) from two proximal fragments (specimens R.9093, 9094) and two distal fragments (specimens R.9095, 9096). It is a slender bone and has been reconstructed to be, as is normal, slightly longer than the ulna. The proximal end is slightly convex, the distal end slightly concave.

A single complete right *ulna* is known (specimen R.9098, Text-fig. 9). The bone is fairly slender. Only the horizontal surface of the glenoid notch is represented. Since the whole of the proximal surface of the ulna is preserved (as proved by its covering of cartilage-ornament), the remainder of the sigmoid notch must have been

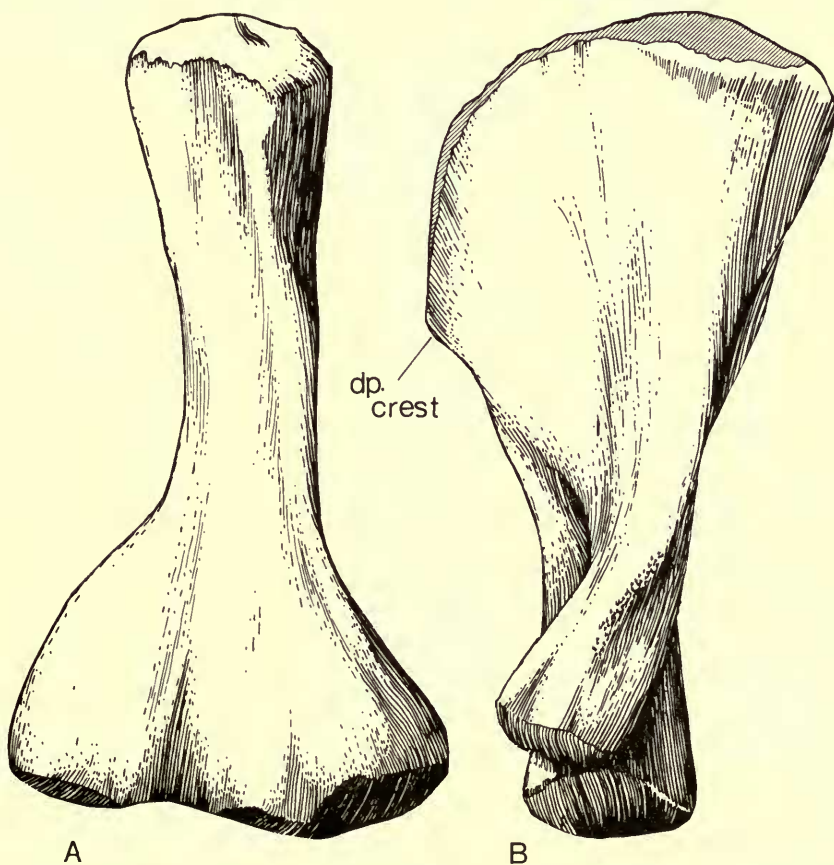


FIG. 8. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Composite restoration of humerus in A, dorsal view and B, anterior view. $\times \frac{2}{3}$. Abbreviations: dp.crest, delto-pectoral crest.

borne on a separately-ossified olecranon process. The distal end of the ulna is strongly convex.

Like those of the pectoral girdle, the bones of the pelvic girdle (Text-figs. 10-12) cannot be fitted together accurately, and much of the regions between the bones must still have been cartilaginous at this stage of growth.

The outline of the *ilium* has been based mainly on that of specimen R.9103, except for the extreme posterior preserved portion of the blade which is taken from specimen R.9106. The sacral facets are reconstructed from specimens R.9103-05.

The outer surface of the blade is slightly concave both dorso-ventrally and antero-posteriorly, while the inner surface is slightly convex in both these planes. The

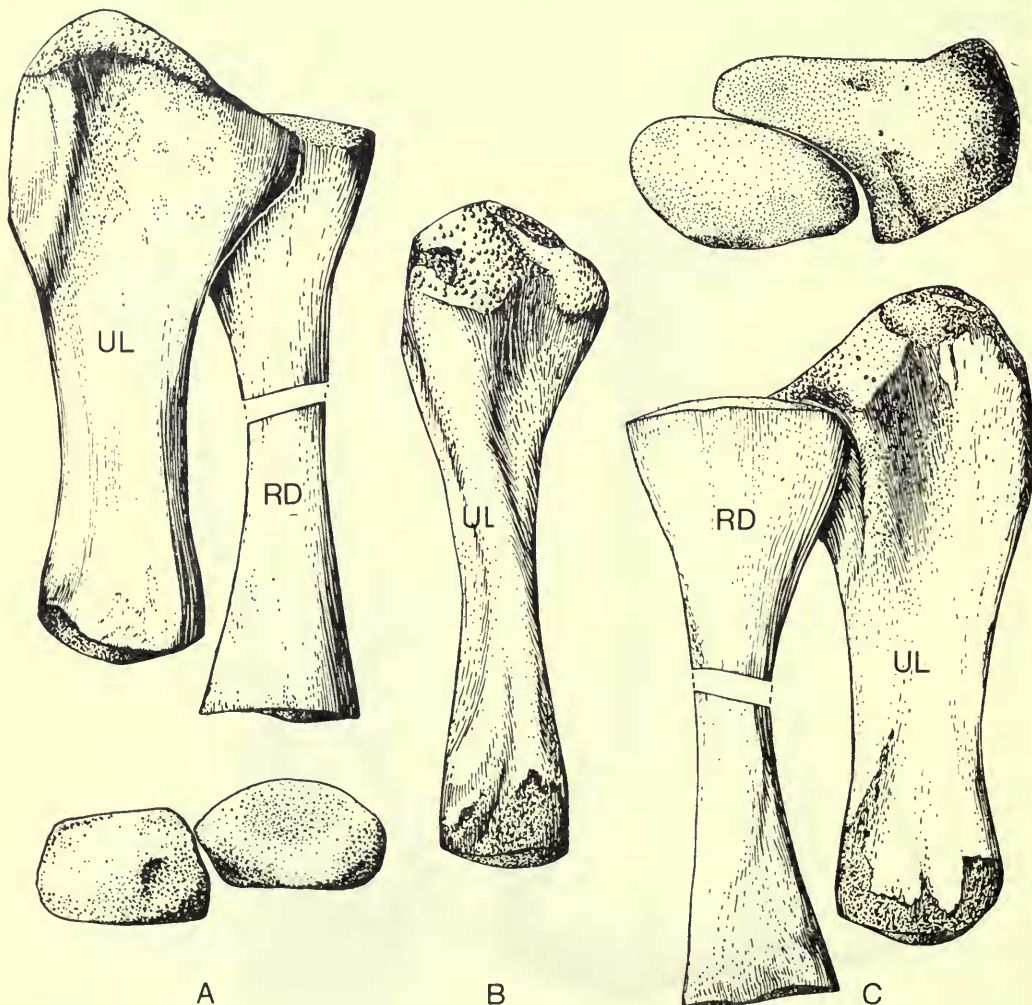


FIG. 9. *Zambiasaurus submersus* gen., et sp. nov., juvenile. A, radius (composite restoration) and ulna in posterior and distal views. B, medial view of ulna; C, radius (composite restoration) and ulna in anterior and proximal views. $\times \frac{2}{3}$. Abbreviations: RD, radius; UL, ulna.

acetabular surface of the ilium faces ventro-laterally and slightly anteriorly. The facets for at least four sacral ribs can be distinguished on the inner surface of the blade (Text-fig. 12).

Most of the outline of the *ischium* (Text-figs. 10, 11) is based upon specimen R. 9108; most of the upper edge and a little of the posterior edge is complete. Specimen

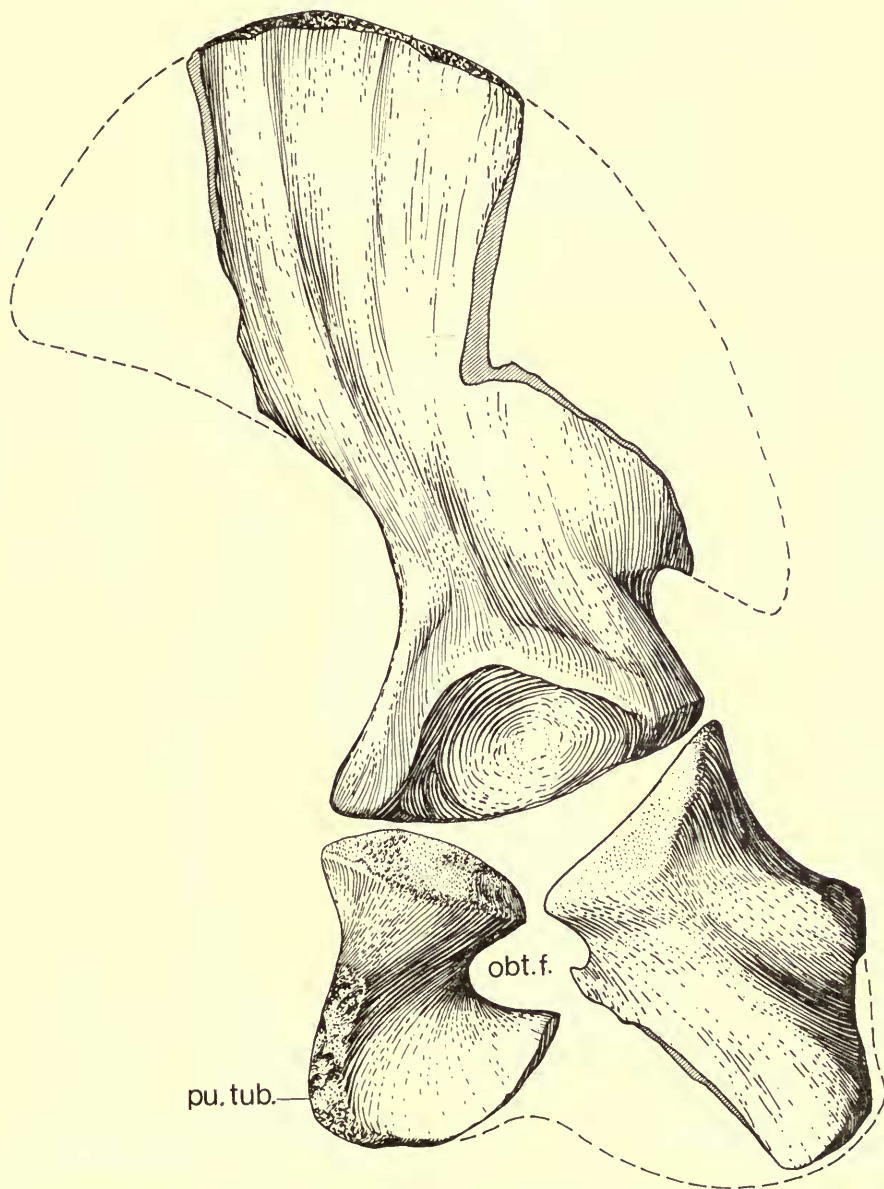


FIG. 10. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Lateral view of pelvis. $\times \frac{2}{3}$.
Abbreviations: obt.f., obturator foramen; pu.tub., pubic tubercle.

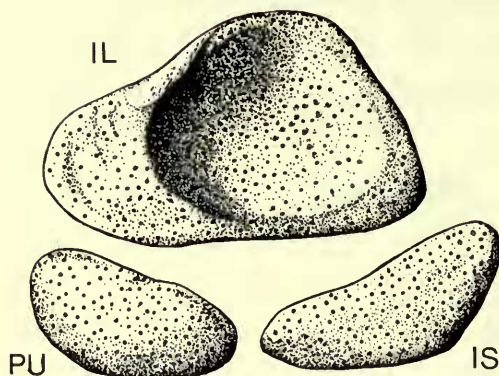


FIG. 11. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Views of acetabular-articulatory surfaces of the ilium (IL), ischium (IS) and pubis (PU). $\times \frac{2}{3}$. Lateral surfaces of the bones are peripheral, medial surfaces are central.

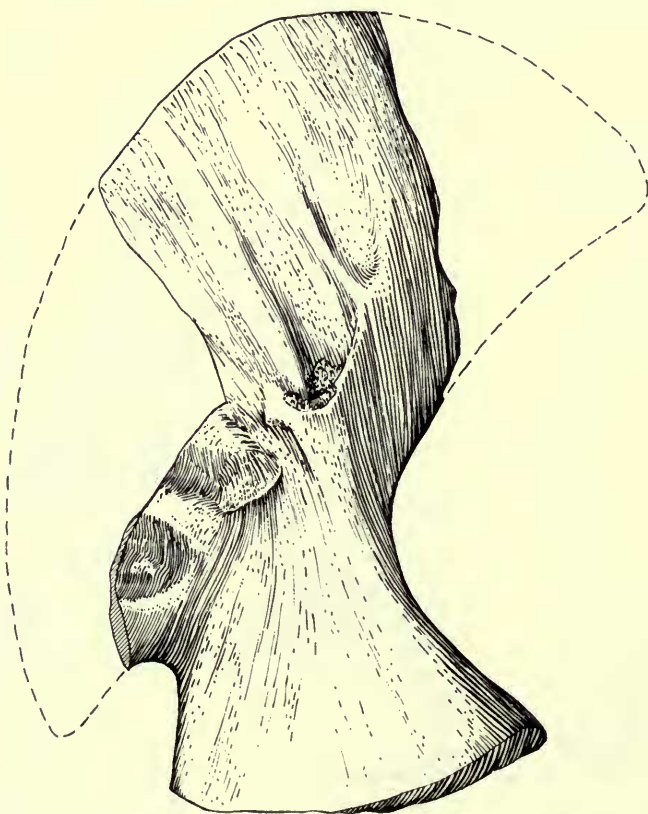


FIG. 12. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Medial view of composite restoration of ilium. $\times \frac{2}{3}$.

R.9109 includes a little more of the ventral portion of the bone. The anterior edge of the ischium is notched for the obturator foramen. The postero-dorsal region of the bone slants somewhat inwards, so that there is a stout ridge between this surface and the more antero-ventral region.

All edges of the *pubis* (specimen R.9113, Text-figs. 10, 11) bear cartilage-ornament, so that the figures show the bone complete at this stage of ossification. It bears a large convex face which must include the surfaces which articulated with the ilium and ischium, and also the pubic contribution to the acetabulum. Below this region the pubis projects antero-laterally to form a rather elongate pubic tubercle. The posterior edge of the bone is notched for the obturator foramen.

The *femur* illustrated (Text-fig. 13) is specimen R.9118, which is complete and from the right side; it is 18.5 cm. long. The articular facets are poorly developed. In side view it can be seen that the distal condyles were probably directed somewhat posterior to the main axis of the bone.

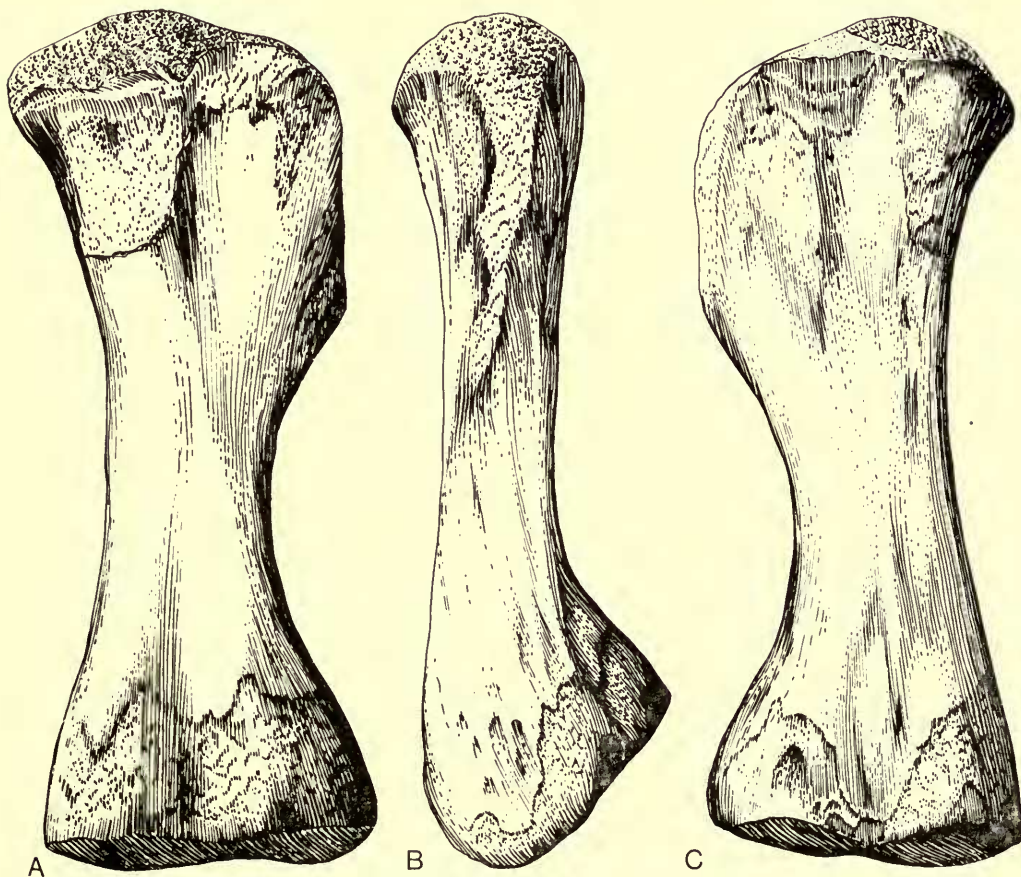


FIG. 13. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Femur in A, anterior view; B, lateral view; C, posterior view. $\times \frac{2}{3}$.

The *tibia* illustrated (Text-fig. 14) is specimen R.9123, which is also complete and from the right side. The proximal surface bears a pair of concavities for the femoral condyles. The lateral surface of this end of the bone is also slightly notched where it adjoined the proximal end of the fibula. The cnemial crest is represented by a thickening of the antero-lateral surface, which ends proximally in a surface which faces slightly anteriorly. The distal surface of the tibia can be divided into a moderately flat lateral region, and a markedly convex medial region.

The *fibula* is a slender, slightly curved bone (Text-fig. 14). The proximal end figured is specimen R.9128, while the distal end is specimen R.9129. The proximal end is convex; it is crescentic in outline, so that its medial edge curves around the lateral surface of the tibia. The distal articular surface is also convex, but is oval in outline.

Though a number of elements from the hand and foot are preserved, no useful information can be derived from them.

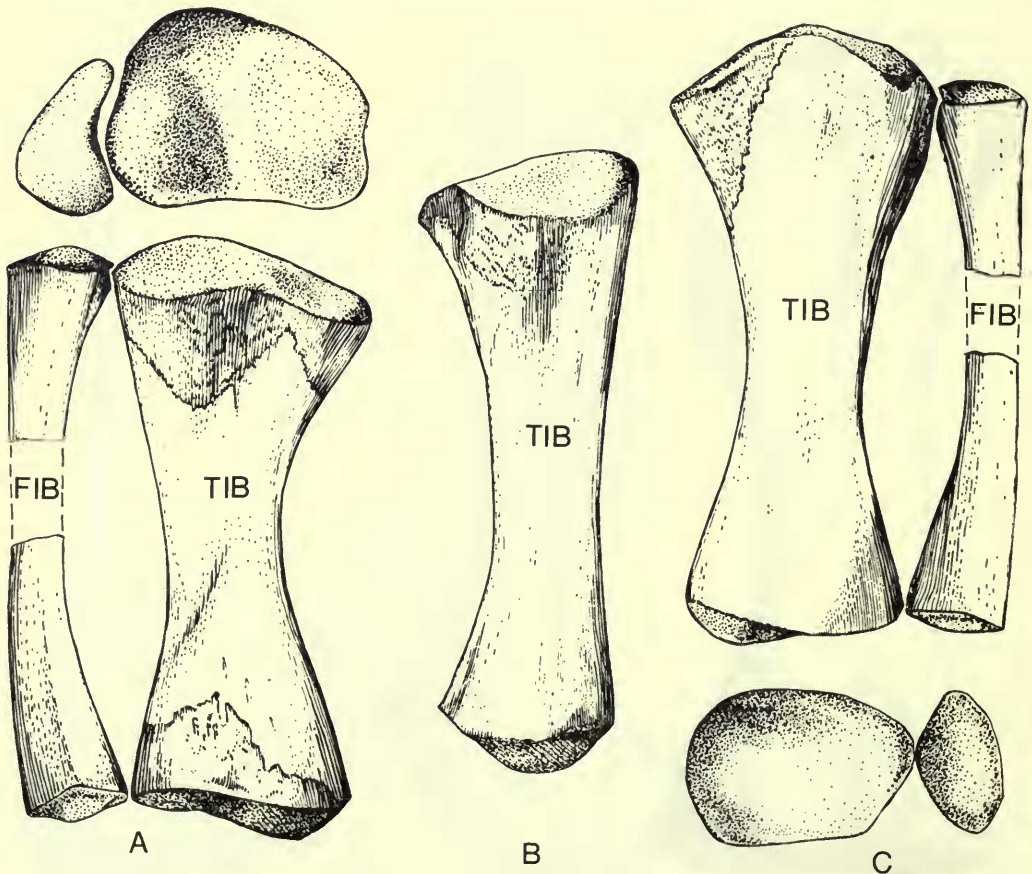


FIG. 14. *Zambiasaurus submersus* gen. et sp. nov., juvenile. A, tibia and fibula in posterior and proximal views; B, medial view of tibia; C, tibia and fibula in anterior and distal views. $\times \frac{2}{3}$. Abbreviations: FIB, fibula; TIB, tibia.

ADULT SPECIMEN. Together with the remains of the immature specimens, there was preserved also a number of much larger dicynodont bones. Since no individual bone was duplicated, and since all of these bones were of commensurate size, it seems likely that all are derived from a single individual. They have therefore all been allocated a single specimen number, R.9140. They include a few uninformative fragments of skull and ribs, a few neural arches, two vertebral centra, a complete left coracoid and fragments of a pair of scapulae, a left humerus, a right radius, ulna and tibia, and a single phalanx.

One of the neural arches is almost complete, and is shown (Text-fig. 15) mounted upon one of the centra. The rib facet extends from the corner of the centrum up the

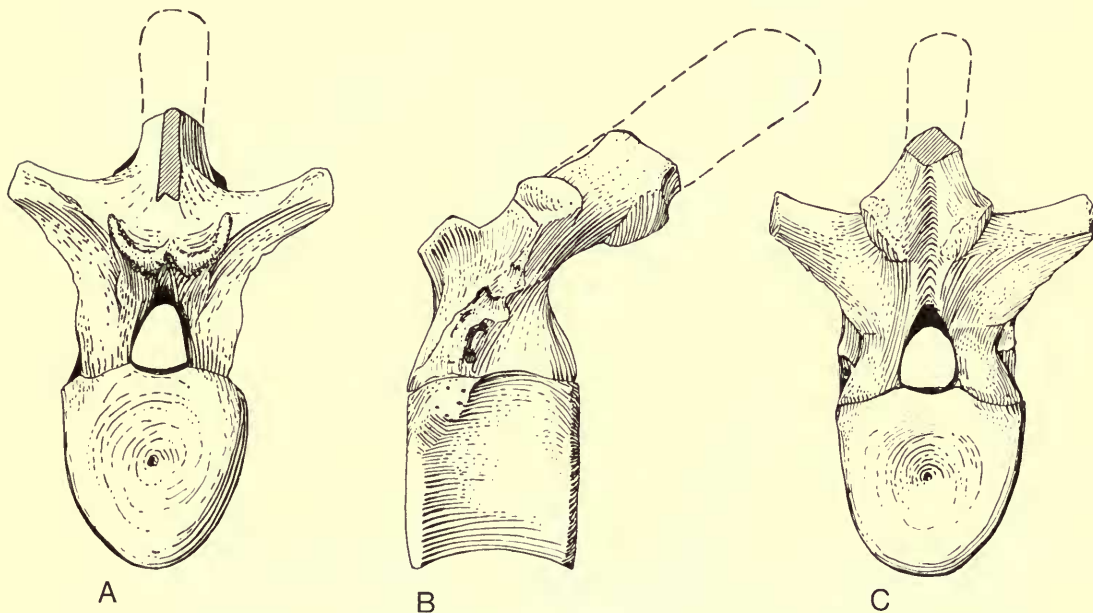


FIG. 15. *Zambiasaurus submersus* gen. et sp. nov., adult (R.9140). Neural arch and centrum (not originally associated) in A, anterior view; B, lateral view; C, posterior view. $\times \frac{1}{2}$.

side of the dorso-laterally directed transverse process, but does not reach its distal end. The outline of the dorsal end of the neural spine is restored from another specimen from this large individual. It is rather narrow antero-posteriorly, and slopes backwards at a considerable angle.

The outline and morphology of the scapula (Text-fig. 16) and coracoid are identical to those of the immature specimen (cf. Text-fig. 4). In anterior or posterior view it can be seen that the blade of the scapula is curved to conform to the outline of the rib cage.

A fragment of the postero-dorsal corner of the proximal end of the humerus is preserved and shows a well developed articular condyle (Text-fig. 17a). The distal half of the bone (Text-fig. 17b, c) shows well developed condyles for the radius and ulna.

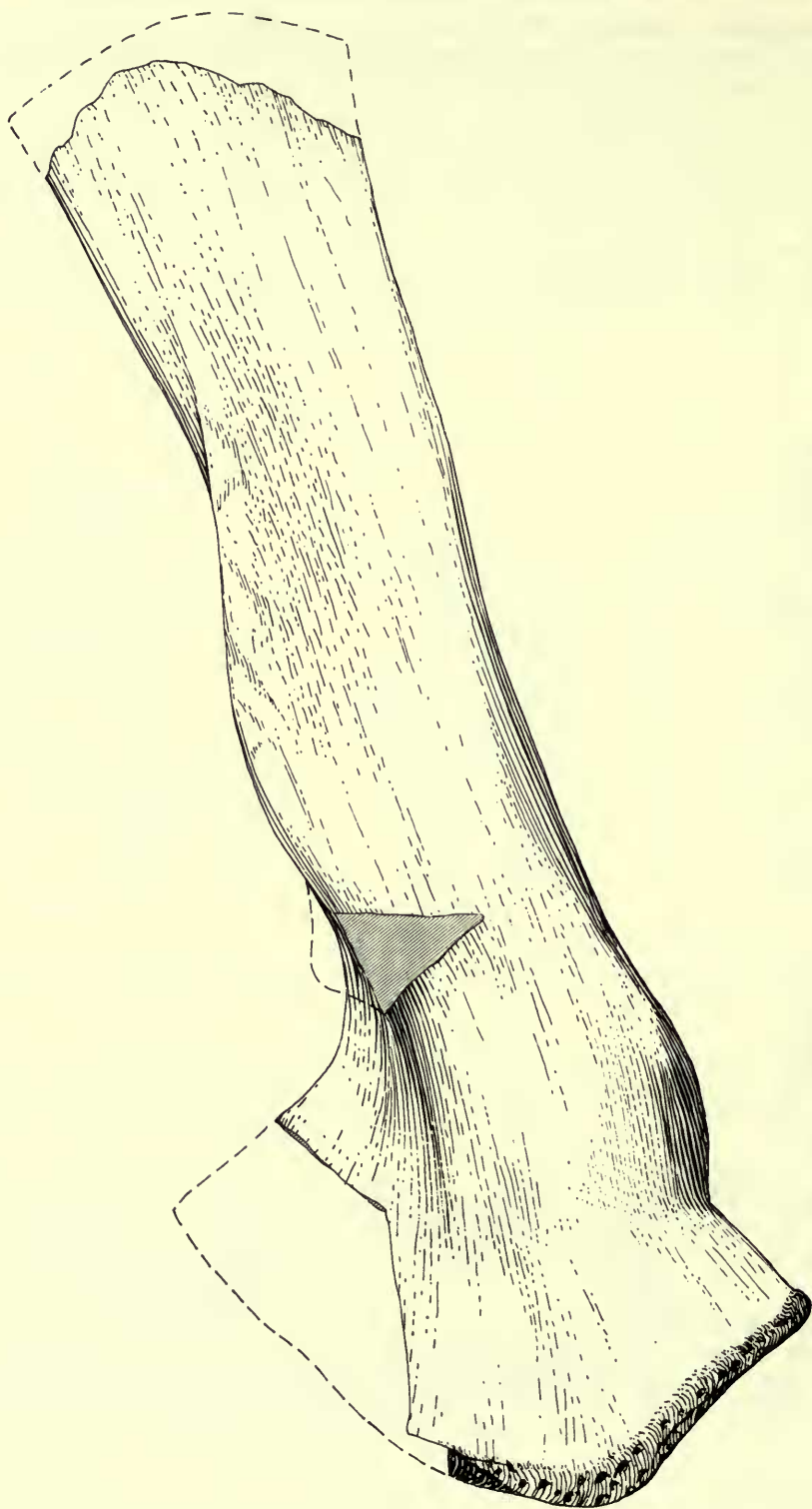


FIG. 16. *Zambiasaurus submersus* gen. et sp. nov., adult (R.9140). Lateral view of scapula, a little less than $\times \frac{1}{2}$.

The proximal ends of the radius and ulna, and the distal end of the ulna, are preserved. This fragment of radius shows no features of interest. The olecranon region of the ulna is lacking, and the proximal surface of the remainder of this end of the bone is unfortunately too poorly preserved for it to be possible to ascertain whether there was a separate olecranon ossification, as in other Triassic dicynodonts.

The proximal end of the tibia is well preserved (Text-figs. 18, 19). The pair of depressions for the femoral condyles are clearly visible. The cnemial ridge running up the antero-lateral face of the bone is better developed than in the immature specimen (cf. Text-fig. 14), and terminates in a rounded surface which is directed dorsally and anteriorly. A rugose area (Text-fig. 19, rug.) on the postero-lateral

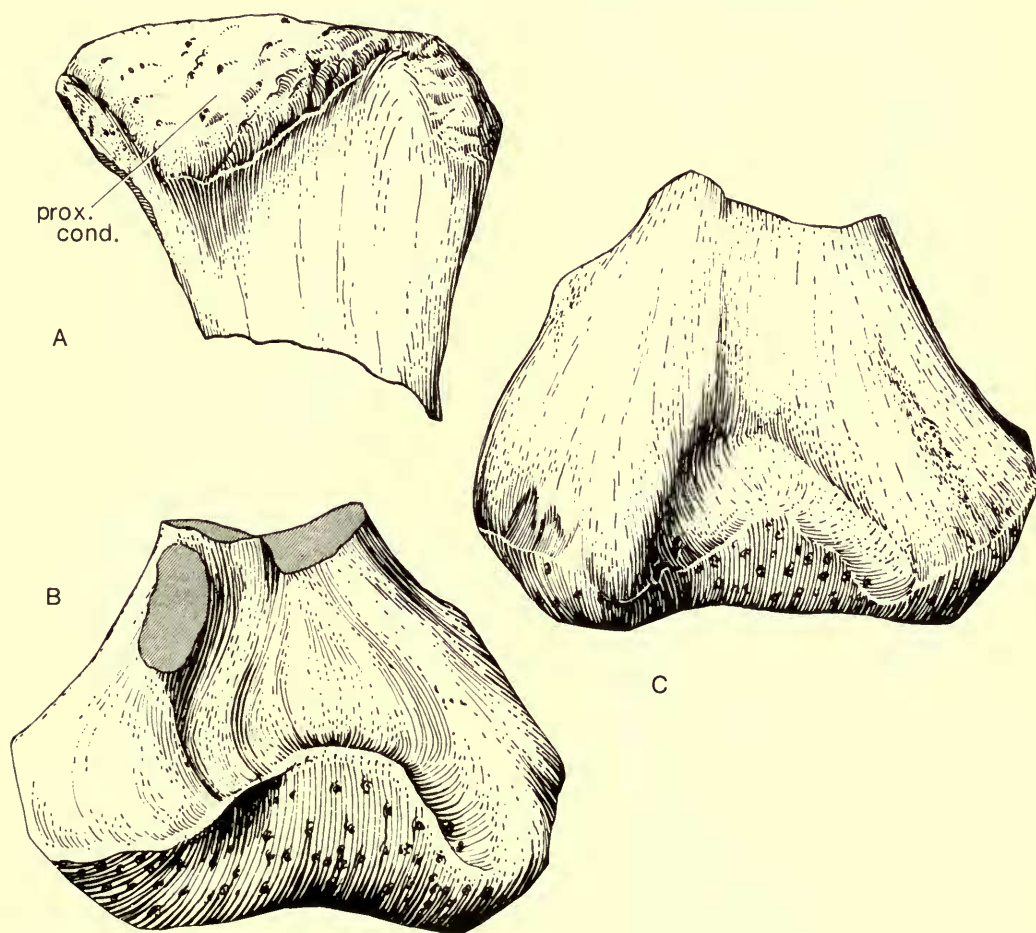


FIG. 17. *Zambiasaurus submersus* gen. et sp. nov., adult (R.9140). Humerus, $\times \frac{2}{5}$. A, B, dorsal views of fragments (A) of proximal end and (B) of distal end; C, ventral view of fragment of distal end. Abbreviation: prox. cond., proximal condyle.

corner of the bone may mark the position where the proximal end of the fibula contacted the tibia.

If measurements (in cm.) of the bones of the adult are compared with those of the immature specimens figured, the following results are obtained.

	Juvenile	Adult	Adult/ Juvenile
Length of scapula	24	43	1·8
Length of coracoid	6·3	10·5	1·7
Width of distal end of humerus	9	17	1·9
Width of proximal end of radius	4·6	10	2·2
Width of proximal end of tibia	5·0	10·5	2·1

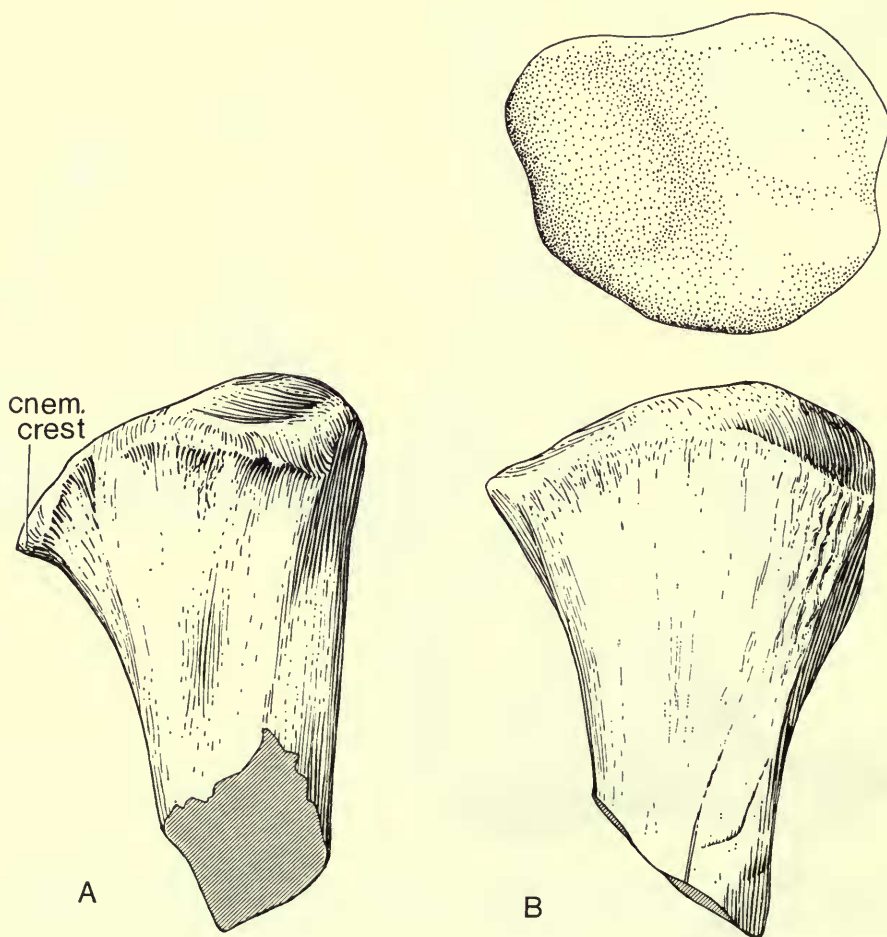


FIG. 18. *Zambiasaurus submersus* gen. et sp. nov., adult. (R.9140) Tibia. $\times \frac{1}{2}$. A, medial view; B, anterior and proximal views. Abbreviation: cnem. crest, cnemial crest.

It can be seen that the adult bones are about twice the size of the juvenile bones. If the skull of the adult was, similarly, about twice the size of the restored juvenile skull and retained a similar length : width ratio, it would have been about 45 cm. long and 40 cm. wide across the occiput.

DISCUSSION. *Taxonomy and relationships of Zambiasaurus*. There can, first of all, be little doubt that *Zambiasaurus* is a stahleckerioid, rather than a kannemeyerioid. Its blunt snout, wide but low occiput, short temporal opening and lack of a

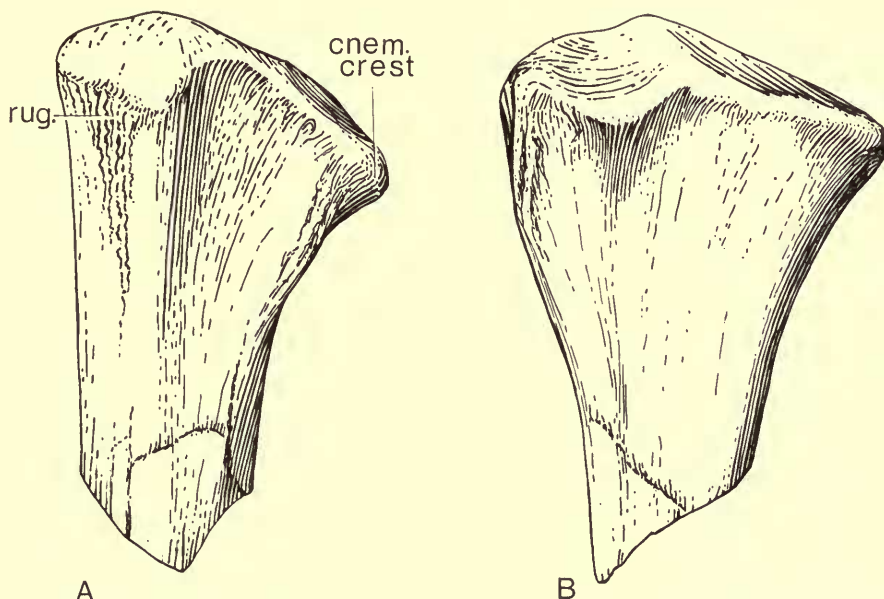


FIG. 19. *Zambiasaurus submersus* gen. et sp. nov., adult (R.9140). Tibia. $\times \frac{1}{2}$. A, lateral view; B, posterior view. Abbreviation: cnem. crest, cnemial crest; rug., rugosity.

high intertemporal crest, are all similar to these diagnostic features of the family Stahleckeriidae as originally defined (Cox, 1965).

Zambiasaurus is the first stahleckerioid known outside South America. The Stahleckeriidae at present includes three genera: *Stahleckeria* of the Santa Maria Formation of Brazil, described by von Huene (1935-42); *Dinodontosaurus* from the above Brazilian Formation (Cox, 1965) and also from the Chañares Formation of Argentina (Cox, 1968) and *Chanaria*, also from the latter Formation (Cox, 1968). Both *Dinodontosaurus* and *Chanaria* have retained tusks and a preparietal bone, in contrast to *Stahleckeria* in which both these features are absent. Their absence in *Zambiasaurus* suggests that this new genus is more closely related to *Stahleckeria* than to the other two stahleckerioid genera.

Though tusks are frequently lost in dicynodonts, the absence of the preparietal is more rare. Comparison of the skulls of *Zambiasaurus* and *Stahleckeria* (Text-fig. 20) reveals several other similarities. Despite some superficial differences, the morphology of the whole intertemporal bar is very similar in the two genera. The parietals in *Zambiasaurus* can still be seen anterior to the pineal foramen, where they have occupied the space normally filled by the preparietal. In *Stahleckeria* the

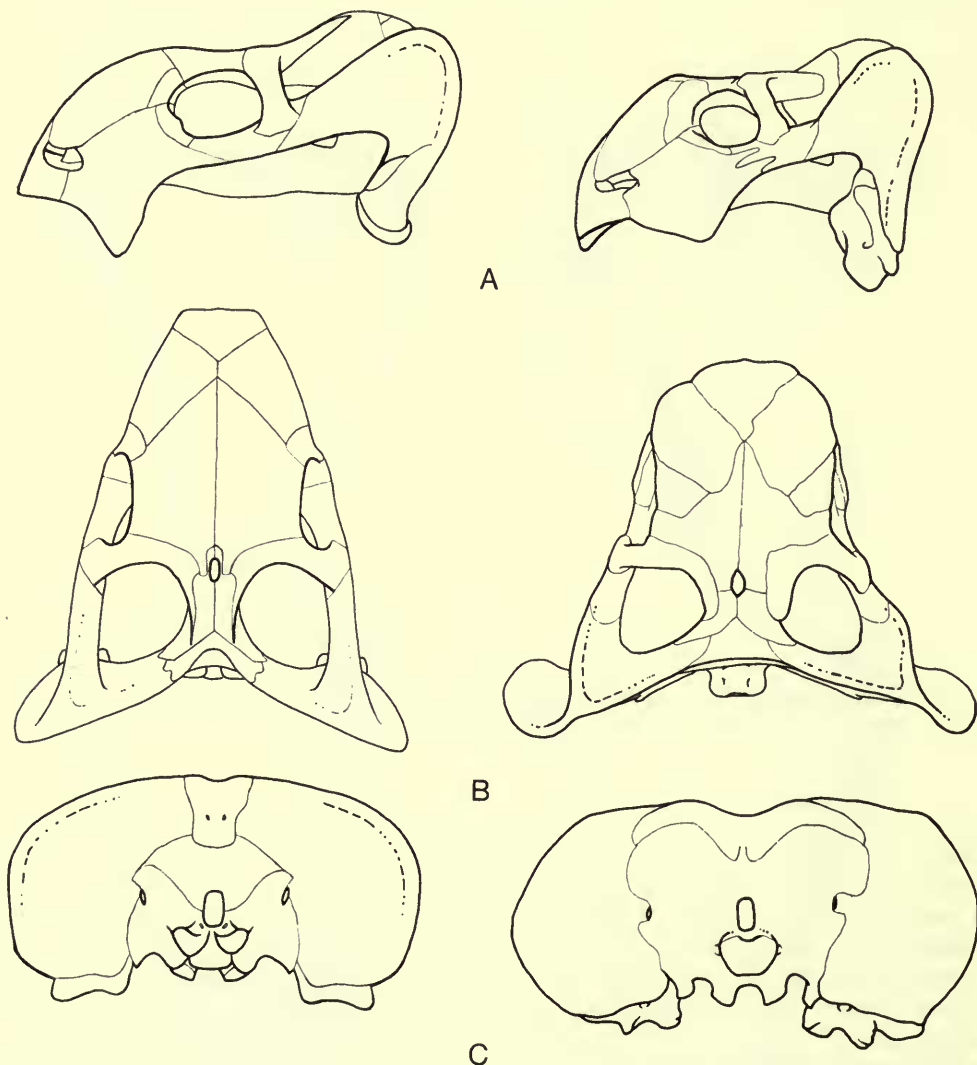


FIG. 20. *Zambiasaurus submersus* gen. et sp. nov., reconstructed juvenile skull $\times \frac{1}{4}$ (left) and *Stahleckeria potens*, adult skull $\times c. \frac{1}{12}$ (right). A, lateral views; B, dorsal views; C, occipital views. (*Stahleckeria* after Camp, 1956).

frontals have extended slightly further back, enclosing the anterior half of the pineal foramen. In both genera the frontal meets the parietal at a level half way along the pineal foramen, the parietal forms a rather wide intertemporal bar which is almost flat in transverse section, and the interparietal contributes little to the intertemporal bar.

Another similarity between *Zambiasaurus* and *Stahleckeria* is that in both the nasals either meet for only a very short distance in the midline or are separated by a junction between the frontals and the premaxilla. In *Stahleckeria* this is probably a result of the very wide, massive snout; if the nasals lie far apart, the processes of ossification outwards from the centre of each bone might not reach the midline before this area had been ossified by the frontal. As far as one can tell, the snout of *Zambiasaurus* also was rather wide; this follows from the shape of the incomplete nasals, and the centre of ossification of the bone certainly lies more lateral than these fragments.

As far as the post-cranial skeleton is concerned, it is in any case difficult to find many systematic differences between the Triassic dicynodonts (see Cox, 1965 for a general survey). This difficulty is compounded in *Zambiasaurus* by the fact that most of the bones are known only in their juvenile state, with poorly developed processes for muscular insertion and articular condyles. A few similarities between *Zambiasaurus* and *Stahleckeria* can nevertheless be observed. The narrow, posteriorly-directed neural spine of *Zambiasaurus* (Text-fig. 15) is very like that of the anterior vertebrae of *Stahleckeria*. The coracoid, sternum and pelvis are in general similar in the two genera, there being a striking similarity between the ischium and pubis of *Zambiasaurus* and those of a juvenile *Stahleckeria* figured by von Huene (1935-42, Pl. 9, fig. 4). The difficulties mentioned above make it impossible to make useful comparisons between the limb bones of the two genera.

The absence of tusks, and of the preparietal bone, the morphology of the intertemporal bar and of the snout, and some post-cranial features thus all suggest that *Zambiasaurus* may be quite closely related to *Stahleckeria*. The Ntawere Formation, in which *Zambiasaurus* is found, is certainly older than the Santa Maria Formation, which contains *Stahleckeria*. It is therefore possible that *Zambiasaurus* may be actually ancestral to *Stahleckeria*, and the known differences between the two genera may now be examined with this possibility in mind.

As far as one can tell, the occipital wings of the squamosal are directed more posteriorly in *Zambiasaurus* than in *Stahleckeria*, so that its occiput is not as flat as that of *Stahleckeria*, and its temporal opening is slightly longer. The occiput itself, as restored, is not as wide in *Zambiasaurus* as in *Stahleckeria*. However, this feature could not, from the material preserved, be restored with any great degree of accuracy. It is also worth noting that the restored skull is that of a juvenile and that the occiput apparently does increase in relative size as the animal grows. This is suggested by the relatively larger occiput of the large specimen of *Dinodontosaurus turpior* which was described as a possible "old bull" (Cox, 1965, pp. 489-494).

Another difference between the occiputs of the two genera is that the interparietal of *Stahleckeria* may extend further laterally, as shown in Camp's (1956) reconstruction

based on further study of von Huene's material. However, the outline of this bone is shown dotted in his figure (1956, Fig. 45) and this point is therefore uncertain. In any case, there is no obvious reason why the interparietal should not become wider during the evolution of the very wide occiput of *Stahleckeria*.

The snout of the "old bull" *Dinodontosaurus* mentioned above is also more massive than that of the smaller specimens, and this should be borne in mind when comparing the immature skull of *Zambiasaurus* with the adult skull of *Stahleckeria*, as these show a similar difference. The snout of *Stahleckeria* is extremely heavy and short, so that the centre of the maxilla lies under the anterior edge of the orbit. As reconstructed, the maxilla of *Zambiasaurus* lies further forwards. However, the exact inter-relationship between its maxilla and orbit cannot be determined from the fragments available (cf. Text-fig. 2) and, in any case, the condition shown in *Zambiasaurus* could well be ancestral to that found in *Stahleckeria*.

The interorbital region of *Stahleckeria* also differs somewhat from that of *Zambiasaurus* in that its nasal and prefrontal extend further posteriorly, so that the anterior half of the upper margin of the orbit is formed by the prefrontal instead of by the frontal as in *Zambiasaurus*. This, too, may be a result of the shorter snout of *Stahleckeria*, since the centres of ossification of the bones of this region must lie further posteriorly, so that they will encroach on the area formerly occupied by the frontal.

The only obvious difference between the post-cranial skeletons of *Zambiasaurus* and *Stahleckeria* is the shape of the scapula. In *Stahleckeria* (von Huene, 1935-42, Pl. 7, figs. 1-3) the scapula narrows above the glenoid region, but further dorsally it becomes progressively wider; there is a strong, antero-laterally directed acromion process, from which a stout spine runs up the outer surface of the blade near its anterior edge. In *Zambiasaurus*, on the other hand, the scapula does not expand dorsally, probably had a small anteriorly directed acromion process, and has a very low spine. However, there is no reason to suppose that the above features of the scapula of *Stahleckeria* could not have evolved from the condition found in *Zambiasaurus*.

To summarize, none of the known differences between the two genera precludes the possibility that *Zambiasaurus* is not only closely related to *Stahleckeria*, but is also directly ancestral to it. It is impossible, on the basis of present material, to test this hypothesis further; such tests will depend on the discovery of stahleckeriids of an age intermediate between that of the Ntawere Formation and that of the Santa Maria Formation.

Origin of the stahleckeriids. As will be shown later in this paper, the age of the Ntawere Formation may provisionally be estimated as lower Anisian. *Zambiasaurus* is therefore the oldest known stahleckeriid. As has already been shown, it is also probably ancestral to *Stahleckeria* and less closely related to the tusked genera *Dinodontosaurus* and *Chanaria*. The line leading to these tusked stahleckeriids must, then, have diverged from the tuskless *Zambiasaurus-Stahleckeria* line in or before the Lower Triassic (Scythian).

I have earlier (1965) suggested that the stahleckeriids (including all the above genera) may be separated from the kannemeyeriids on the basis of the form of the

palate and occiput. The morphology of these areas is, of course, determined by the orientation and volume of the jaw muscles, and by the way in which the jaws are used during feeding. The modifications in the kannemeyeriid line (seen most clearly in *Kannemeyeria* and *Ischigualastia*) seem mainly to be directed towards increasing the antero-posterior length of the jaw muscles. This has been achieved by some exaggeration of that posterior extension of the squamosal which is common in Permian dicynodonts, and also by the postero-dorsal extension of the posterior region of the inter-temporal bar. These features seem to accompany a rather pointed premaxilla (e.g. *Sangusaurus*, see Text-fig. 22b) in which the anterior ends of the paired anterior palatal ridges of the premaxilla meet the converging lateral walls of the mouth cavity. As a result of this, the grooves which lie lateral to these ridges meet the antero-lateral margins of the snout, not its anterior edge.

The modifications of the stahleckeriids, instead, seem to have been directed towards an increase in the width of the skull and anterior end of the jaws. The posterior extension of the squamosal is lost altogether and the temporal opening is very short, but that part of the squamosal which lies lateral to the root of the zygomatic arch is greatly developed. This lateral development presumably provided attachment for muscles which would have allowed more accurate control of the lateral movements of the jaw than would have been possible in the kannemeyeriids. This may be correlated with the transversely widened anterior surface of both the premaxilla and the dentary. As a result of the width of this region, the paired palatal ridges of the premaxilla, and the grooves lateral to these ridges, run on to the anterior edge of the snout (Text-fig. 3d).

I have earlier (1965) suggested that these differences may be explained by their feeding habits, the kannemeyeriids having been browsers feeding on fronds and leafy branches, while the stahleckeriids were grazers, feeding on any low herb-cover similar to that provided by grasses today. Further understanding of the functional mechanical differences between these two groups will be possible only when well preserved undistorted skulls and jaws are available. These would permit the study of the sequences of possible jaw movements, in the same way as Crompton & Hotton's (1967) investigation of the functional morphology of two Permian dicynodonts, *Emydops* and *Lystrosaurus*.

It is at present impossible to suggest confidently any links between the Triassic dicynodont groups and the varied dicynodonts of the Upper Permian Kistecephalus Zone. Immediately above this zone lies the *Lystrosaurus* Zone, in which tiny *Myosaurus* and the aberrant lystrosaurids are the only dicynodonts known. Above this is the *Cynognathus* Zone from which *Kannemeyeria* is the only dicynodont described. Though the *Sinokannemeyeria* fauna of China is about the same age as the *Cynognathus* Zone fauna (though Bonaparte (1966) had tentatively suggested that the *Sinokannemeyeria* fauna might be younger than this, he no longer considers that this is likely [Bonaparte, personal communication]), the possible kannemeyeriids *Sinokannemeyeria* and *Parakannemeyeria* are very specialized in their long snouts, as Bonaparte (1966) has pointed out, a modification quite unlike the general trend in dicynodont evolution.

As a result of these facts, little can be said of the history of the stahleckeriids and

the kannemeyeriids during the Scythian or (if their differentiation had taken place even earlier) during the late Permian. Dicynodonts with both the high, narrow type of skull (e.g. *Daptocephalus*, *Dinanomodon*) and the low, wide type of skull (e.g. *Aulacephalodon*) are found in the Upper Permian Kistecephalus Zone fauna of South Africa. There may or may not be phyletic connections between these Permian forms and the corresponding Triassic groups; it is, at present, impossible to decide.

Genus ***SANGUSAURUS*** nov.

DIAGNOSIS. Large dicynodont: complete skull would probably have been 35–40 cm. long. No teeth in upper or lower jaws. Premaxilla tapers anteriorly to blunt point. Median region of intertemporal bar markedly concave in transverse section. Low boss immediately posterior to pineal foramen. Interparietal forms posterior end of intertemporal bar.

TYPE SPECIES. *Sangusaurus edentatus* sp. nov.

Sangusaurus edentatus sp. nov.

Text-figs. 21–23

HOLOTYPE. Livingstone Museum (Zambia) specimen No. LM/NH 9/1 (Field No. 15 H/4) consisting of the following damaged bones: premaxilla, right and left maxillae, right and left quadrates; postero-dorsal corners of both squamosals; right prefrontal; intertemporal bar, consisting of interparietal and right and left parietals.

HORIZON AND LOCALITY. Upper fossiliferous horizon of Triassic Ntawere Formation; from locality 15 of Drysdall & Kitching (1963), about 3½ miles west of Sitwe, in the upper Luangwa Valley, Eastern Province, Republic of Zambia.

DESCRIPTION. The material was collected as isolated fragments over an area of about 50 square yards but, since all the bones are of commensurate size and no individual element is duplicated, it seems very likely that all belong to a single skull. Though much of this skull was not recovered, the fragments preserved are sufficient to demonstrate that it belongs to a new genus of dicynodont. The generic name *Sangusaurus* is derived from that of a nearby stream, the Sangu, while the specific name *edentatus* refers to the lack of tusks.

The most characteristic feature of the new genus is the intertemporal bar (Text-fig. 21). The median region of the parietals is quite deeply concave in section, as can be seen in posterior view (Text-fig. 21c). The sides of this trough form ridges, parts of the lateral surfaces of which may have been originally covered by the post-orbitals, though the bone is too badly damaged for the areas of overlap to be distinguishable.

There is a low, median rugose boss immediately behind the pineal foramen. The anterior ends of the parietals are damaged, but what remains of these surfaces

bears a pattern of vertical grooves similar to those found at the anterior end of the parietal of *Zambiasaurus* (cf. Text-fig. 1e). This suggests that these surfaces are those to which the frontals and preparietal were sutured.

The interparietal forms a wide contribution to the posterior end of the intertemporal bar and has a W-shaped suture with the parietals. There is an abrupt transition between this region of the interparietal and its occipital region (Text-fig. 21b, occ. surf. ip), since these two regions lie at a very acute angle ($c. 25^\circ$) to one another. As preserved, the occipital surface of the interparietal therefore slopes very sharply antero-ventrally, and it seems unlikely that this is due to crushing, since this region of the skull is extremely solid. If it is undistorted, this orientation of the occipital surface of the interparietal implies that the whole intertemporal

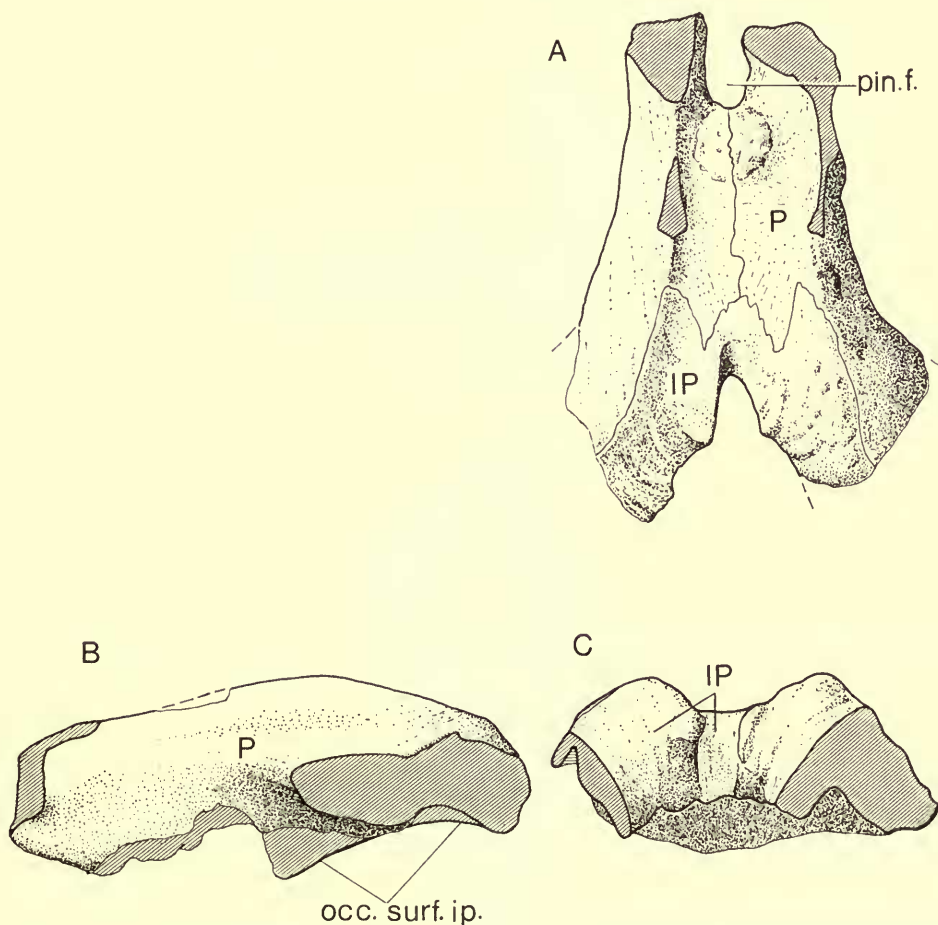


FIG. 21. *Sangusaurus edentatus* gen. et sp. nov., intertemporal bar of type specimen. $\times \frac{1}{2}$. A, dorsal view; B, lateral view; C, posterior view. Abbreviations: IP, interparietal; occ.surf.ip., occipital surface of interparietal; P, parietal; pin.f., pineal foramen.

bar was directed postero-dorsally, so that its posterior end projected backwards above the occiput.

The palatal surface of the premaxilla (Text-fig. 22b) bears a pair of anterior palatal ridges. The premaxilla tapers anteriorly, so that the anterior ends of these ridges meet the converging lateral surfaces of the bone. The grooves lateral to these ridges therefore do not emerge along the anterior edge of the premaxilla, but along its antero-lateral edges, and they are more shallow than the median groove which lies between the palatal ridges. The outer surface of the anterior end of the premaxilla bears a median ridge and a pair of lateral ridges.

The right maxilla (Text-fig. 3) is more complete than the left. There is no sign of a tusk either in the caniniform processes or in either maxillary antrum. A fairly well developed flange runs down the postero-lateral edge of the bone. The

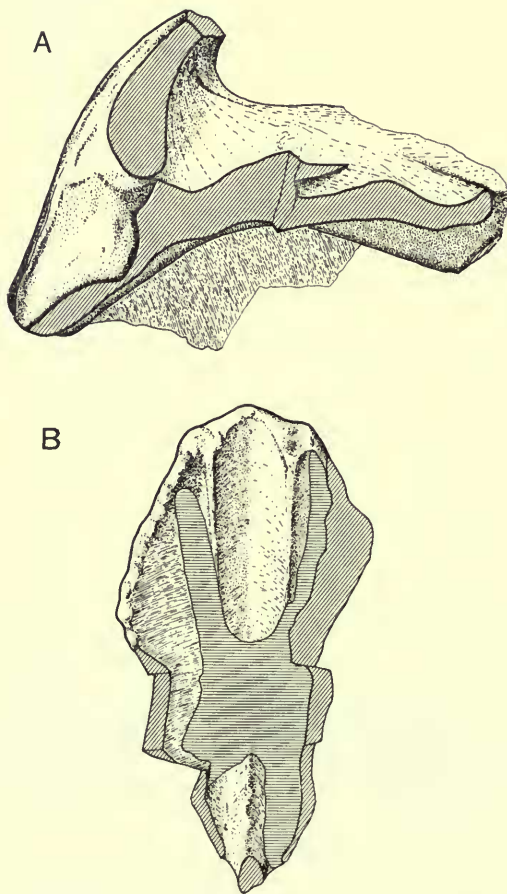


FIG. 22. *Sangusaurus edentatus* gen. et. sp. nov., premaxilla of holotype. $\times \frac{1}{2}$.
A, lateral view; B, ventral view.

palatal surface of the maxilla is slightly recessed anteriorly where it would have been overlapped by the premaxilla. If the maxilla is orientated so that its caniniform process is directed vertically, the ventral edge of this recess runs antero-ventrally at a considerable angle to the horizontal. However, the premaxilla-maxilla suture in this region in most dicynodonts runs approximately horizontally, parallel to the palatal surface. Such a result can be achieved only if the caniniform process is swung forwards so as to have a very marked antero-ventral orientation.

The isolated right prefrontal and a few other damaged and unidentifiable fragments show no features of significance.

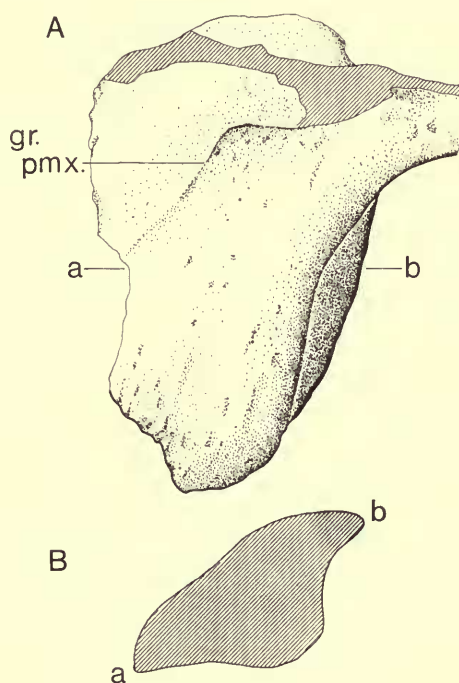


FIG. 23. *Sangusaurus edentatus* gen. et sp. nov., maxilla of holotype. $\times \frac{1}{2}$. A, lateral view; B, section through maxilla at a-b. Abbreviation: gr.pmx., groove marking lower limit of area of maxilla originally covered by premaxilla.

DISCUSSION. *Taxonomy and relationships of Sangusaurus.* There can, first of all, be no doubt that *Sangusaurus* is generically distinct from all other dicynodonts, since the features mentioned in the diagnosis are not found together in any previously known genus.

Several features indicate that *Sangusaurus* is a kannemeyeriid rather than a stahleckeriid. These features include the postero-dorsally directed intertemporal bar (if the posture of this region has been interpreted correctly above) and anteriorly tapering premaxilla, the palatal ridges of which meet the lateral edges of the bone,

not the anterior edge. The well developed flange down the posterior surface of the maxilla is also commonly found in kannemeyeriids (though a small flange is present in the stahleckeriid *Zambiasaurus*).

The Kannemeyeriidae at present includes six genera: *Kannemeyeria*, from the Lower Triassic Cynognathus Zone of South Africa, the Middle Triassic Manda Formation of East Africa, and the Middle(?) Triassic Puesto Viejo Formation of Argentina (Bonaparte, 1966, 1967); *Sinokannemeyeria* and *Parakannemeyeria*, both from the Lower Triassic Er-ma-ying Formation of Shansi, China; *Barysoma*, from the Middle Triassic Santa Maria Formation of Brazil; *Ischigualastia*, from the Middle or Upper Triassic Ischigualasto Formation of Argentina, and *Placerias* from the Upper Triassic Chinle Formation of Arizona, U.S.A. The morphology of *Ischigualastia* and *Placerias*, and the inter-relationships of all the above genera have been discussed in an earlier paper (Cox, 1965).

Compared with the above kannemeyeriids (except *Barysoma*, whose skull is known only from a partial occiput), the structure of the intertemporal bar of *Sangusaurus* is closest to that of *Ischigualastia*. In both genera the median region of the parietals is concave in transverse section, there is a W-shaped suture between the parietals and the interparietal, and the posterior end of the intertemporal bar (again, if correctly interpreted in *Sangusaurus*) projects posteriorly above the occiput. The intertemporal bars of the other genera differ. That of *Placerias* is much wider than that of *Sangusaurus* and is flatter dorsally in cross-section. That of *Kannemeyeria* is very narrow, forming a sharp median crest. Those of both *Sinokannemeyeria* and *Parakannemeyeria* are moderately wide and are concave dorsally, but are not postero-dorsally directed, and there is therefore a more gradual transition from the dorsal surface of the intertemporal bar on to the occiput.

Though similar to one another in general, the intertemporal bars of *Sangusaurus* and *Ischigualastia* differ in that the interparietal is much longer in *Ischigualastia* and forms the whole width of the posterior end of the intertemporal bar, and the dorsal surface of its interparietal is convex, not concave as in *Sangusaurus*.

Another similarity between *Sangusaurus* and *Ischigualastia* is the lack of tusks in both genera. All the remaining kannemeyeriids are tusked. (This region is unknown in *Barysoma*, which appears to be closely related to *Ischigualastia*.) However, this similarity is less significant than the similarities noted above, as many dicynodont genera have lost the tusks. If the antero-ventral orientation of the caniniform process of *Sangusaurus* suggested above is correct, this is another feature known only in this genus and in *Ischigualastia*.

The above comparisons suggest that *Sangusaurus* is more closely related to *Ischigualastia* than to the other known Triassic kannemeyeriids. However, *Sangusaurus* is so incompletely known that it would be unwise to place too much reliance upon these resemblances, or to regard a relationship between the two genera as definitely established.

IV. AGE OF THE NTAWERE FAUNAS

Before the significance of the faunas of the Ntawere Formation can be appreciated, it is first necessary to establish the Triassic faunal sequence into which they must be

inserted. I shall therefore first discuss the faunas and ages of three other units: the Cynognathus Zone of South Africa, the Molteno Beds of South Africa and the Manda Formation of Tanganyika (Tanzania).

1. *Cynognathus Zone*. This is the uppermost unit of the Beaufort Series. The fauna includes cynognathid, diademodont and trirachodont cynodonts, the very primitive rhynchosaurs *Howesia* and *Mesosuchus*, and the primitive pseudosuchians *Euparkeria* and *Erythrosuchus*. The only dicynodont which has been described is *Kannemeyeria*; however, two other undescribed genera are known, one in the collection of the Bloemfontein Museum, South Africa, and the other in that of the Smithsonian Institution, Washington. Though the Cynognathus Zone is up to 2,000 feet thick, this fauna is found only in the lowest 500–600 feet (Hotton & Kitching, 1963).

I have recently (Cox, 1967) suggested that the Cynognathus Zone may be best regarded as of Upper Scythian age. This estimate was based upon the presence in the underlying Lystrosaurus Zone (itself regarded as Lower Scythian in age) of the capitosaurid labyrinthodont *Wellugosaurus*, which had also been identified from a bed in Greenland above a zone containing a dateable ammonite fauna. Though Welles & Cosgriff (1965) have pointed out the unreliability of the Greenland specimens in particular, and of this "genus" in general, Cosgriff has also provided a better basis for the dating of the Cynognathus Zone. He has described (Cosgriff, 1965) a new Australian temnospondyl which is associated with microfloras and marine fossils, both of which indicate a Lower Scythian age. It is closely related to *Peltostega* of the Upper Scythian Poisdonomya Beds of Spitzbergen, and to *Rhytidosteus* of the Cynognathus Zone. Cosgriff (1965) also points out that comparison of the temnospondyl amphibians of the Cynognathus Zone with those of the Lystrosaurus Zone suggests that there was probably an appreciable time lapse between these two faunas. Relevant here is Hotton & Kitching's (1963) comment, based on geological interpretation, that the Cynognathus Zone may have been deposited after a considerable interval of erosion. All these facts may be reconciled and accommodated if the Lystrosaurus Zone is regarded as of Upper Permian age (as Cosgriff, 1965, suggests), and is followed by a gap in the record, equivalent to the Lower Scythian, which is in turn followed by the Upper Scythian fauna from the lower part of the Cynognathus Zone.

2. *Molteno Beds*. These beds were originally regarded as barren. Boonstra (1947) described a cynognathid cynodont, *Cynidiognathus longiceps*, collected by Stockley in what he thought were lower Molteno Beds of Basutoland (now Lesotho). This species is known from the Cynognathus Zone, and it is now thought possible that this specimen may have come from nearby exposures of that Zone. More recently, Crompton & Ellenberger (1957) described a traversodont cynodont, *Scalenodontoides*, from the upper Molteno Beds; however, Crompton (1968, personal communication) now considers that the level from which this specimen originated lies in the strata which are transitional between the Molteno Beds and the overlying Red Beds, not in the typical Molteno Beds. As a result, once again, vertebrate fossils are unknown from the Molteno Beds. These beds, up to 1,900 feet thick, may therefore cover all or part of the time between the underlying Upper Scythian

Cynognathus Zone and the overlying Red Beds. These latter contain a varied dinosaur fauna, including melanorosaurs, thecodontosaurs and sauropod-like footprints, and are probably of Upper Triassic age (Charig, Attridge & Crompton, 1965). No more accurate assessment can at present be made than that the Molteno Beds therefore represent part or all of the Middle Triassic (Ladinian and Anisian).

3. *Manda Formation*. This fauna lacks the more primitive cynognathid and diademodont cynodonts found in the Cynognathus Zone, but instead includes traversodont cynodonts. Both the rhynchosaur and the diverse pseudosuchians are far more advanced and common than are those of the Cynognathus Zone. The dicynodonts include a greater variety of forms than the Cynognathus Zone, but the genus *Kannemeyeria* is still present. The Manda fauna has provisionally been regarded as of Anisian (possibly Upper Anisian) age (Cox, 1965, 1967).

4. *Ntawere Formation*. As already mentioned, this formation contains two fossiliferous horizons, which will be discussed separately. That from the lower part of the formation contains two undescribed new tusked dicynodonts (in the collection of the Bernard Price Institute for Palaeontological Research, Johannesburg), the cynodont *Diademodon rhodesiensis*, and fragments of large labyrinthodonts. The age of this fauna must at present depend upon the characters of the cynodont. Brink (1963 : 79) states that this is "very typically a *Diademodon* and it is very difficult to find a particular feature about the skull on the strength of which it can emphatically be differentiated from a known species like *D. polyphagus*" (of the Cynognathus Zone). Brink notes, however, that the post-dentary bones are more reduced, and the coronoid process of the dentary better developed, than in the Cynognathus Zone species. These somewhat advanced features may indicate that this Ntawere fauna is slightly younger than that of the Cynognathus Zone, and it might conveniently be regarded as equivalent to the upper, non-fossiliferous, portion of the Cynognathus Zone.

The upper fossiliferous horizon extends over the topmost beds of the Ntawere Formation and the lower part of the Red Marl. Its fauna includes the stahleckeriid dicynodont *Zambiasaurus*, the kannemeyeriid dicynodont *Sangusaurus*, two traversodont cynodonts (*Luangwa drysdallensis* Brink 1963 and another specimen which will be described by Crompton), fragments of pseudosuchians, and the remains of the largest known labyrinthodont amphibian, approximately twice the size of *Paracyclotosaurus* (which will be described by Panchen).

The absence of diademodonts (as far as is known), the presence of traversodonts and its stratigraphical position above the lower fossiliferous horizon (itself of possible Cynognathus Zone affinities) all indicate that this upper Ntawere fauna is younger than the Cynognathus Zone. The above characters of its cynodont fauna similarly indicate a closer relationship to the Manda fauna. The only remaining problem is whether this Ntawere Fauna should be regarded as older than, or the same age as, the Manda Formation. The only fact relevant to this decision is the absence from the Ntawere fauna of the rhynchosaurs which form such a large element in the Manda fauna. Though, as has been pointed out previously (Cox, 1967), this group is notably unreliable as a faunal indicator, it must be accepted here in the absence of any more

reliable evidence. The upper fossiliferous horizon of the Ntawere Formation is therefore provisionally to be regarded as slightly older than the Manda Formation. If this is so, the suggestion of Dixey (1936) and of Drysdall & Kitching (1964) that the Escarpment Grit (which underlies the Ntawere Formation) may be equivalent to the Kingori Sandstone (which underlies the Manda Formation) must be incorrect unless the Kingori Sandstone is equivalent to both the Ntawere Formation and the Escarpment Grit. It is, perhaps, more likely that the Kingori Sandstone represents a later phase in the sedimentary cycle which began with the Escarpment Grit.

TABLE I

	South Africa	Zambia	Tanzania
Rhaetian	Cave Sandstones		
Norian	Red Beds		
Carnian	} Molteno Beds		
Ladinian			
U. Anisian			Manda Formation
L. Anisian		Ntawere Formation	Kingori Sandstone
	Unfossiliferous		
U. Scythian	U. Cynognathus Zone		
	Cynognathus Zone	Escarpment Grit	
	fauna		
L. Scythian			
U. Permian	Lystrosaurus Zone		
„	Kistecephalus Zone	Madumabisa	Kawinga Formation
		Mudstone	

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